NICHE PARTITIONING IN *LITTORINA OBTUSATA* AND *L.MARIAE*.

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ABSTRACT

Littorina obtusata (L.) and L.mariae Sacchi and Rastelli are congeneric species of gastropod inhabiting similar niches on the rocky intertidal. Both species show clines of morphological variation, and these are described for populations in the Severn estuary. Detailed study was carried out at Sawdern, West Wales.

L.obtusata lives over a wide vertical range, but its optimum niche is at mid shore on Ascophyllum nodosum. L.obtusata is a macro-algal grazer and feeds on the fronds of Ascophyllum. This is a reliable resource and maintains all the stages of L.obtusata's 3-4 year life history.

L.mariae is restricted to low shore on Fucus serratus. It is a micro-epiphyte browser and the timing of its development is linked to the seasonal presence of epiphytes, and the winter die-back of F.serratus fronds. It lives for only one year.

The potential niches of the two species (as determined by abiotic factors) were investigated using caging experiments. These showed that L.obtusata actually grew better when caged at low shore than at mid shore. The potential niche of L.mariae, however, does not include mid shore; physical factors limit its growth at this level.

The realized niches of the two species are maintained by directional movement. Both species homed to their own zone when displaced; while movement within their own zones was random.

Predation pressure by crabs was investigated at low shore. Tethered individuals of both species were voraciously eaten. It is suggested that predation would eradicate L.obtusata populations at low shore due to the vulnerability of the thin-shelled juvenile stages. L.mariae avoids this pressure because it quickly grows a smaller but thicker shell, reaching sexual maturity within a year.

Predation pressure is therefore proposed as the major evolutionary force partitioning the niches of L.obtusata and L.mariae, resulting in the differences in their morphology, life history and ecology.

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MEMORANDUM

The work described in this thesis is my own and has not previously been submitted for consideration for a higher degree at this or any other university. Due acknowledgement has been made in the text of any assistance received.

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CONTENTS

1. INTRODUCTION

1.1 NICHE THEORY

Niche theory and concepts of speciation have always been closely linked. Grinnell (1924) referred to the niche as the ultimate distributional unit of one "species or subspecies." Grinnell further elaborated on his niche concept (Grinnell 1928) emphasizing that the distribution limits of a species distribution were set by environmental barriers. In modern terms, Grinnell described the "pre-interactive niche" of a species (Vandermeer 1972), where the distribution of this species was not limited by biological interactions (in the form of competition, predation etc) but by abiotic influences. The "post-interactive" niche of a species was first suggested by Elton (1927) who described the niche of an animal as being "its place in the biotic environment, its relation to food and enemies" (Vandermeer 1972). Elton illustrated his theory with examples of animal dependence on food habits. The combination of these theories,together with the experimental work of Gause, allowed Hutchinson (1957) to suggest how the niche might be more rigorously defined.

Hutchinson agreed with Grinnell that the distribution of a species was limited by abiotic influences such as temperature and salinity. He viewed these as being variables along whose axis there was a point at which the variable was limiting, being either too small or too large (eg.too cold or too hot), and beyond which a species could not exist. Between these two points the species was able to exist and reproduce. This represents the

pre-interactive niche or in today's terminology the potential niche of a species. Hutchinson viewed this potential niche as being modified according to biotic variables such as predation and competition. The resultant "volume" is the post-interactive niche of Elton, or the realized niche in Hutchinson's terms. Each variable, whether biotic or abiotic, is viewed as a dimension along which the species is limited. It is virtually impossible to identify all these dimensions and so they can be described as "n-dimensions". When these are all considered the niche of a species can be envisaged as a "hyper-volume" delimited by these initial dimensions within the space of the environment. Therefore the niche of a species can be described as an "n-dimensional hyper-volume in hyper-space" (Hutchinson 1957).

Hutchinson was further able to state that no two species could inhabit the same realized niche. This was a result of Gause's experimental work with Protozoa (Gause 1934). Gause showed, admittedly in an artificial laboratory situation, that if two species competed for a limiting dimension (resource) then equilibrium between the species would not occur. One species would be successful to the exclusion of the other. Although Gause never actually coined the phrase this discovery became known as "Gause's hypothesis" (Krebs 1978) or the "competitive exclusion principle" (Giller 1984). Many ecologists investigated the integrity of this principle in the field. Closely coexisting species were examined because if they "do coexist then there should be some ecological difference between them, implying such species each have their own

unique niche" (Giller 1984). Investigation of such coexisting species could enlighten the scientific view of the niche.

The results of such investigations have proved mixed. Lack (1944) working with British passerine birds and McArthur (1958) working with New England warblers both agreed with the principle, finding partitioning of the birds' morphology, feeding habits and spatial distribution. Ross (1957), however, working with Illinois leafhoppers could find no difference between the niches of 6 species. One problem of investigating this principle is that in many cases more than one dimension may be limiting, and/or being competed for (Krebs 1978). In addition competition may not be taking place and Hutchinson (1957) defined three limits for the Competitive Exclusion Principle, beyond which it would never be expected to occur. Inside these limits competitive exclusion could take place between two species competing for the same limiting resource.

McArthur further investigated this problem according to a reversal of the principle by asking "If complete competitors cannot coexist, how different do two species have to be in order to be in the same habitat?" (Krebs 1978). This method of thinking encompasses the Niche Overlap Concept - the degree of overlap of niches that species can tolerate before direct competition and exclusion occur. Pielou (1972) has illustrated a method for measuring the width of a niche and degree of overlap. It is considered that a degree of partitioning of resources is acceptable until overlap is too large and direct

competition results. Sinker's simple analogy of the niche as a fried egg (Wilson et al. 1983) allows further demonstration of this idea. The Potential Niche inhabited is seen as being the white of a fried egg - this does not represent the entire Potential Niche as Sinker argues that the species performs relatively poorly at the extreme limit of the niche. Competition and predation are viewed as bites out of this fried egg, the yolk being the Optimal Niche. If too many bites are taken out of this "egg" then the species will be forced to "move" to a different place and avoid competition or change their ecology to avoid competition (Krebs 1978).

This effect of competitive exclusion may lead to speciation. The movement of a species to another area to avoid competition can result in members of that species becoming geographically isolated from the other members of the species in the original habitat. Reproductive barriers may ensue because hybrids between the two groups are poorly adapted and are therefore selected against, and two species may result. This is a form of allopatric (or geographic) speciation, an example of which is found in the platyfishes of Central America (Xiphophorous maculatus species group). Species are recognized by differences in micro and macromelanophore patterns which occur from stream to stream. A gradient of speciation is shown in these fish from a local genetic race, to an ordinary subspecies, to an almost specifically distinct subspecies, to a full species (Mayr 1970). If an ecological movement takes place sympatric speciation may occur dividing the ecologically diverging populations into different species. Sympatric

speciation has been described as "speciation without geographic isolation" (Mayr 1970) and is based upon two main prerequisites. First, the new populations of "species" must be established and exist in different ecological niches where they are differentially selected. Second, as a result of their relative selective advantages, a reproductive barrier will arise preventing gene flow between these two populations. Many examples of sympatric speciation are thought to occur. Mayr (1970) quoted the case of the genus Perdita (a bee genus) in N.America which encompasses almost 500 species of bee. These live in the same area, and are all oligolectic, but either feed on different species of plants, or visit the same species of plant but at different times. The limiting ecological resources are therefore partitioned between the species.

1.2 WINKLE SPECIATION

A group of species generally regarded as being the result of sympatric speciation is that of the periwinkles of rocky shores (Barnes and Hughes 1982). The zonation of periwinkles along the vertical axis of the beach is seen as illustrating sympatric evolution by ecological separation and subsequent reproductive isolation of the winkles present. The examples quoted as illustrating this phenomonen are the high shore Littorina neritoides, mid shore L.saxatilis and L.littorea and the lower shore L.littoralis . This nomenclature was considered correct until 15 years ago when investigation showed this to be a very simplified picture (Heller 1975, Raffaelli 1982). Certainly L.neritoides and L.littorea are distinct species which have different ecological niches, do not interbreed

and may well have originated as a result of sympatric speciation. This is not the case in L.saxatilis and L.littoralis, both of which are now considered to be species complexes; a species complex being a group of species which look very much alike in most morphological features (Krebs 1978).

Littorina saxatilis (the rough periwinkle) is the best documented, least understood and most argued over "species" of winkle. The number of species considered to exist in this complex has varied greatly since taxonomists decided that certain morphological forms of this winkle warranted specific status. One of the first workers to tackle this problem was James (1968) who attempted to classify the winkles according to their digenean parasites. Using this method he described five subspecies and ten varieties of L.saxatilis. The next major work on the "saxatilis complex" appeared in 1975 when Heller attempted their classification. His classification was based on shell morphology, colour pattern, anatomy of reproductive tract, radula morphology and isoenzyme pattern. Taking advantage of the early separation of L.nigrolineata by Sacchi (1975), Heller (1975) described four species- L.rudis, L.patula, L.nigrolineata and L.neglecta - which he claimed to be fully sympatric. Further investigation by Raffaelli (1979) disputed some of Heller's work and considered L.patula to be synonymous with L.rudis. This opinion was also held by Hannaford-Ellis (1979) who designated a further species, L.arcana,(1978) on the evidence that it was oviparous compared with the ovoviviparous L.rudis, the name under which it was

previously classified due to shell morphology.

The number of winkle species thought to form the "saxatilis complex" in 1979 was four - L.rudis, L.nigrolineata, L.arcana,and L.neglecta. In 1981 J.E.Smith further investigated the complex and claimed that L.rudis and L.saxatilis , previously considered to be synonymous, or different geographic forms, were different species. This classification had posed great difficulties due to the loss of Linnean type specimens for L.saxatilis collected by Olivi. Many workers regarded L.saxatilis as the Mediterranean form of the rough periwinkle and L.rudis as the northern form. J.E.Smith (1981) supported this view on investigating winkles from the type locality for L.saxatilis of Venice. Subsequent work by Fretter and Graham (1980) and Raffaelli (1982) regarded L.rudis as being the extreme of a cline of variation and classified the species as L.saxatilis due to this name having taxonomic priority. Recent work by Janson (1982 , 1983) has provided evidence to support this clinal variation in morphology of L.saxatilis.

Raffaelli (1982) provided a review of the classification of littorinids following Fretter and Graham (1980) who described the present state of taxomomy regarding winkle species, recognizing L.saxatilis, L.arcana, L.neglecta and L.nigrolineata. This authoritative text recognized L.neglecta and L.nigrolineata as "good species" (as confirmed by gene enzyme patterns investigated by Wilkins & O'Regan (1980) and Caugant & Bergerand (1979)) but described L.arcana, L.saxatilis (and L.tenebrosa) under one section, illustrating the continuing confusion

regarding their status. Further ecological investigation has thrown light on other possible species; such as the variety of L.rudis, described as var.scotia, found in Rockall by S.Smith (1979). Recently Ward and Janson (1985); and Janson and Ward (1986) have clarified the status of L.arcana (as a separate species) and L.tenebrosa (as a variety of L.saxatilis).

The "L.saxatilis complex" does not directly concern this project but is a useful comparison with the study subject, and on which to reflect. The "L.saxatilis complex" illustrates the difficulty in assigning diagnostic characteristics on which to base species' classification . According to whether morphology, ecology or reproductive isolation are given the greatest weight, different species are erected. As Mayr (1976) commented "one taxomomist might call species every polymorph variant, a second one every morphologically different population, and a third one every geographically isolated population".

The speciation of winkles should therefore be treated with great care and scepticism; the relative changes in shell/radula morphology and even reproductive mode may only reflect responses to environmental effects (and may possibly be stages in sympatric speciation) but may not result in reproductive isolation or warrant specific status.

1.3 FLAT PERIWINKLES

The species studied in this project are the flat periwinkles, the taxonomy of which, like L.saxatilis, is confused. The confusion stems from the original placing of two similar shells in two different taxa by Linnaeus in

1758 (Goodwin and Fish 1977). Many workers followed this example and described new species for extremely different shells, judged on morphological features, resulting in a rich and varied number of species in the flat periwinkle group. In 1914 Dautzenberg and Fischer reduced these to one species, L.obtusata (from Scandinavia) which was described as having L.littoralis as a subspecies (the British form). In 1932 Colman brought these "species" or "subspecies" L.obtusata and L.littoralis under the one name of L.obtusata together with L.palliata (the Arctic and American form) claiming that they all integrated, representing a morphological gradient, and that the name L.obtusata had priority by pagination.

Colman further clarified the classification of flat winkles in 1933 correcting the classification of Gowanloch and Hayes in 1926 who described the winkle as L.palliata. The name L.obtusata therefore became widely accepted and much work was conducted on this "species". The majority of the work was of a somewhat observatory nature (Colman 1933) or concerned with the polymorphism showed by the shells. This aspect was extensively investigated by Sacchi in the English Channel (1961,a,b; 1966,a,b) and also by Dautzenberg and Fischer (1914). These workers commented on a bimodal size (height) distribution; Sacchi (1966 a) referring to normal-sized and dwarf adults and Dautzenberg and Fischer (1914) to a minima form as well as the normal-size form.

In 1966 Sacchi and Rastelli reviewed the differences between the dwarf and normal-size flat periwinkles and concluded that they represent different species, L.obtusata

being the normal-sized form and L.mariae (Sacchi and Rastelli 1966) being the dwarf form. The separation of "L.obtusata" into two different species was based on a number of features. The first of these was the difference in height of shell, long suspected as exhibiting a major difference between the two forms (Sacchi 1966), L.mariae being the smaller form and having a more rheophilous shell. The shells of the two species also had different colour morph frequencies. The third point concerned the morphology of the male genitalia. The penises of the species differed, L.obtusata having a large glandular area with two or three rows of penial glands and a short filament, whereas L.mariae had a short glandular area, with one row of penial glands and a larger whip-like filament. Sacchi and Rastelli considered this to be a very important diagnostic character as it could result in reproductive isolation of the species. Sacchi also further differentiated the two species, showing L.mariae to exhibit greater sexual dimorphism than L.obtusata (Sacchi 1967, 1968,) and less tolerance to physical extremes (Sacchi 1972a and b).

Subsequently investigation has confirmed the original findings of Sacchi and Rastelli. The most significant modern contribution to the morphological characterisation of these species and their identification was made by Reimchen 1974, and Goodwin (1975), reviewed by Goodwin and Fish (1977). These works showed that adults of the two species have significant differences: the spire L.mariae is more flattened than that of L.obtusata; the colour of the ovipositor of L.mariae is unpigmented, while

that of L.obtusata has black pigment; the radula morphology of the species differ in the number and location of cusps and the colour morph frequencies differ in that L.obtusata is usually green (Olivacea) and L.mariae is usually yellow (Citrina). There was also an important difference in the juveniles of the species, based on shell morphology. Reimchen suggested differences in the two species' ecologies based on differential mortality affecting colour polymorphism and shell size. More evidence of the specific status of these winkles was given by Wilkins and O'Regan (1980) who showed by isoenzyme studies that L.obtusata and L.mariae significantly differ at both loci for the enzymes phosphoglucose isomerase and phosphoglucomutase.

It is therefore widely accepted that L.obtusata and L.mariae are separate species of flat periwinkle. Despite this, as a result of the confusion in the taxonomy of the "L.saxatilis" complex, the taxonomy of L.obtusata and L.mariae has come under review with regard to the possibility of other species in the complex. S.Smith (1978) and Reimchen (1974 and 1981) have both described dwarf forms of L.mariae for which S.Smith coined the term "L.mariae beeensis" (Fretter and Graham 1980). A similar "subspecies" has also been described for L.obtusata, namely L.aestuarii Jefferys, which was claimed to be an estuarine form of its marine relative. Detailed electrophoretic isoenzyme investigation by Moyse, Thorpe and Al-Hamadini (1982) has shown no significant difference between the gene enzyme systems of L.obtusata and L.aestuarii. Moyse et al. therefore considered L.aestuarii to be synonymous with L.obtusata. S.Smith followed a similar view with the

relationship between "L.mariae beeensis" and L.mariae claiming that L.aestuarii and "L.mariae beeensis" could be regarded as "ecomorphs" of L.obtusata and L.mariae (Smith pers. comm). Smith (1982) also stated that the name L.mariae should be replaced by the more senior synonym L.fabalis, from Turton's collection (Turton 1825); althoug h this has been refuted by Sacchi (1984).

The relative simplicity of this pair of species, as compared with the L.saxatilis complex, has recently spurred many workers to investigate them. Original work on shell colour polymorphism by Sacchi (1968) has been furthered by J.E.Smith (1976), with regard to L.obtusata, and Reimchen (1974) for both species and with particular regard to predator-related crypsis (Reimchen 1979). Reimchen (1981) was still doubtful about the individuality of the species L.mariae and suggested the possibility of a second species. Further ecological work has been carried out by Guiterman (1970) on the population biology of L.obtusata; and Goodwin (1978) investigated the reproductive aspects of this species and the reproductive similarity with Lacuna pallidula. Goodwin (1975), as previously mentioned, provided a detailed study on intra- and interspecific variation of L.obtusata and L.mariae. Other aspects of these winkles which have been recently investigated include the isoenzyme work of Moyse et al. (1982) and Wilkins & O'Regan (1980) and the chromosome-number count by Janson (1983).

The current knowledge of these species therefore seems rich; but it is to be remembered that much of the early work is discredited by the discovery that taxa

originally treated as one species in fact consists of two species. As a result almost all the work before 1966 has to be reviewed very critically, and even some work after 1966 is subject to question as a result of classificatory confusion. The division of L.obtusata into two species has been ignored by some workers. Daguzan (1978) in relating the morphological, anatomical and physiological adaptations of the Littorinidae to the different shore levels they inhabit described L.obtusata and L.mariae under the name L.littoralis and briefly mentioned the possibility of a species complex. The value of these works is therefore questionable. The recent literature is in fact somewhat sparse, and very little is known of the basic ecology of these animals. Much of the previous work has been concentrated, almost to the point of obsession, on colour polymorphism without knowledge of their feeding habits, dispersal and other basic ecological aspects of their life histories; one of the most important of which must be their inter-relationship.

It is the aim of the present work to redress this inbalance. These two species pose a fascinating ecological problem. They appear to be sympatric species existing in almost identical niches. They appear to share the same shore levels; the same food plants; the same reproductive modes and similar life histories. It is known that L.obtusata shows a preference for a higher tidal level than L.mariae and different weed species to "feed" on, but this is only the result of field observation and has been the subject of little detailed research. This work will attempt to investigate the ecology of these animals,

examining their niche, or niches, to understand how they inter-relate and divide the resources available. An investigation of this nature will also question the evolutionary significance of this relationship and hopefully provide evidence about possible sympatric speciation of these animals. Through detailed ecological investigation it should be possible to define the partitioning of the niche(s) inhabited by these animals and shed some light on their specific existence.

2. SITES

The distribution of the two species of flat periwinkle was investigated along the Severn Estuary. From this initial survey sites for further ecological work were chosen. The initial survey showed that L.obtusata extended as far up the Estuary as Aust whereas L.mariae only reached Brean on the English coast and Sully on the Welsh coast. The winkles' distribution was limited to that of their host weed species. Due to this reliance the sites chosen needed to have dense weed cover in order to support sufficiently large winkle populations for experimental work. The sites chosen and their location are shown in Figure 2.1.

These sites represent isolated outcrops of weed-covered rock which are separated by different types of substrate such as mud flats and docks etc. The sites on the Welsh coast were Sully and Porthcawl, and the English sites were Aust, Blue Anchor and Porlock. Porlock and Porthcawl were considered to represent the seaward extent of the Estuary (Boyden et al 1977) and Aust is the most estuarine of the sites. A comparative marine site, Sawdern in West Wales, was also chosen. It was hoped that Sawdern would provide a site to complement those on the Estuary.

The sites chosen can be described as follows:

2.2 ENGLISH COAST

2.2.1 AUST

Grid reference : ST 565901

Aspect : NW facing

Ballantine scale : 6

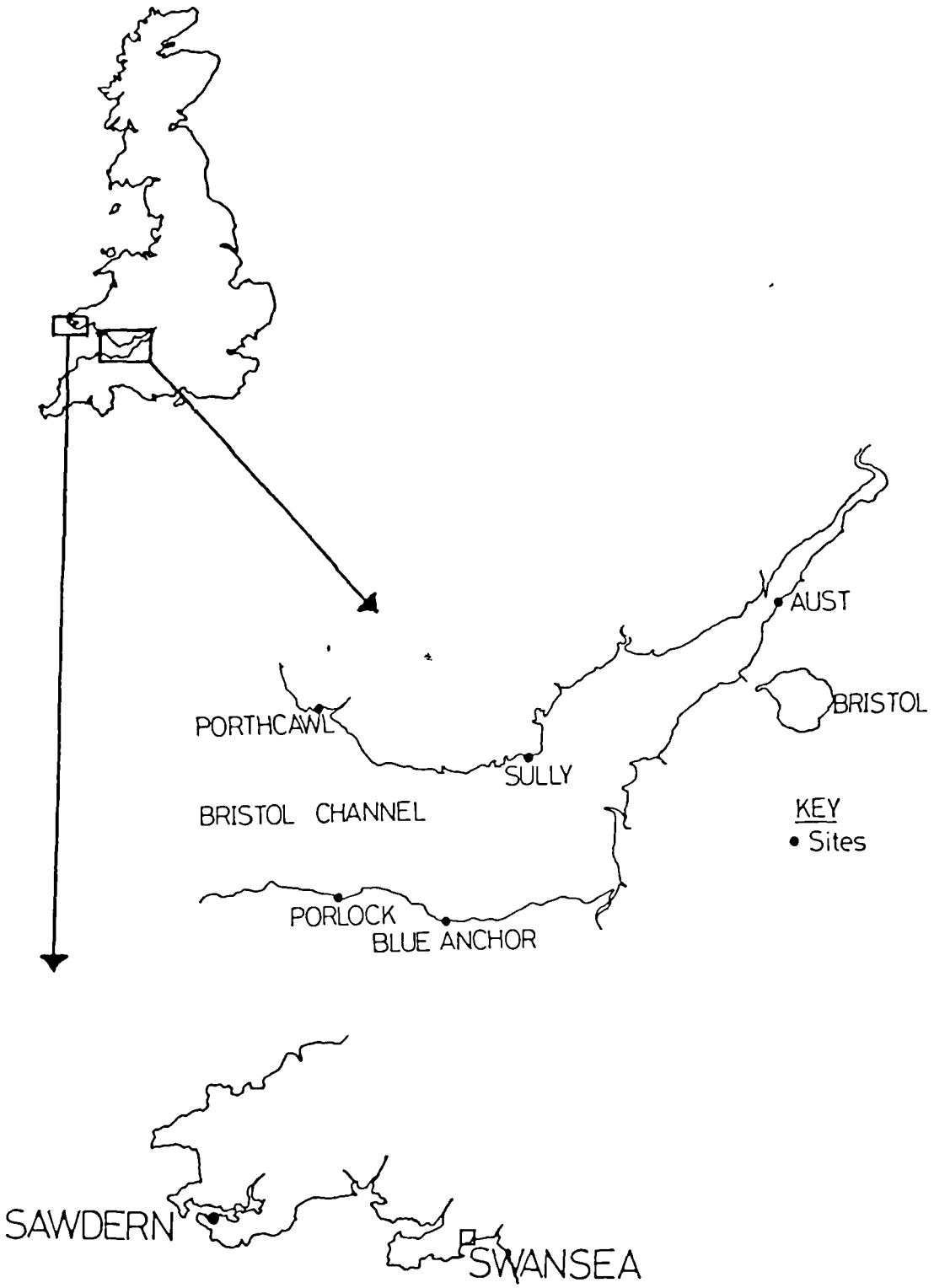


Figure 2.1
Map to show the location of sampling sites (maps not to the same scale)

The upper shore is composed of loose angular boulders. Below MHWN this becomes soft red Keuper Marl. The rest of the shore consists of a long platform of Carboniferous limestone which ends in steep cliffs at low water (see Little and Smith 1980).

As a result of the top of the shore being broken up and irregular the top zoned weeds (after Lewis 1964) were either absent or very sparse. The mid shore section had a very dense covering of Fucus vesiculosus and Ascophyllum nodosum which both grew luxuriantly. At the bottom of the shore Fucus serratus grew well forming dense beds but ending abruptly above low water, below which no weeds extended (for discussion see Little and Smith 1980).

The diversity of the fauna at Aust was very poor, the dominant species being L.obtusata which was found in abundance. This site was the furthest up the Estuary and as such was subject to heavy sediment scour. It was also in the lee of the Severn Bridge which results in periodic disturbance due to renovations.

2.2.1 BLUE ANCHOR

Grid reference : ST 052437

Aspect : N facing

Ballantine scale : 6

The top of the shore was similar to Aust in that it was broken up and often covered in shingle. There was, however,a dense zone of Fucus spiralis on the highest permanent rocks. The mid shore seaweeds were patchy due to the irregular nature of the bed rock, and clumps of F.vesiculosus and A.nodosum were present, rarely forming large beds. The lower shore had dense beds of F.serratus

which extended below MLWN. Again, like at Aust, there was a sharp cut-off point below which no weed grew at the bottom part of the shore.

Faunal diversity was poor, but greater than at Aust; Lacuna pallidula was found at the bottom cf the algal beds.

2.2.3 PORLOCK

Grid reference : SS 857484

Aspect : NW facing

Ballantine scale : 4

Fairly uniform boulder shore (see Bassindale 1943, Wilson *et al. 1983 and Crothers 1976)*.

Porlock had a very low algal diversity and distribution. There were no high shore weeds. At mid tide level stunted F.vesiculosus plants were present merging into F.serratus at the lower part of the shore where the plants were in a better condition. At the bottom of the shore there was an extensive laminaria bed (principally Laminaria digitata).

The fauna at Porlock was extremely rich and diverse being almost totally marine (see Bassindale 1943).

2.3 WELSH COAST

2.3.1 SULLY

Grid reference : ST 165674

Aspect : SSW facing

Ballantine scale : 6

A smooth rocky shore sloping gently towards the sea. Rock ledges are present along the beach (see Purchon 1948).

The flora of this site showed the general weed zonation pattern of sheltered rocky shores, from Pelvetia

to F.serratus. There was a dense bed of Ascophyllum and F.vesiculosus, but at mid/low shore this was patchy. Lower down the shore there were clumps of F.serratus which formed dense beds at low water, beyond this point there was no more seaweed.

The fauna found at Sully was quite diverse although there was still a paucity of marine species.

2.3.2 PORTHCAWL

Grid reference : SS 769845

Aspect : S facing

Ballantine scale : 6

This shore was an irregularly sloping Conglomerate rock platform. At high water this was covered by sand and a shingle storm beach, and at the bottom of the shore the beach breaks up into outcrops of rock surrounded by sand.

As a result of this truncation of the shore Pelvetia was sparse although present. There were good beds of all the other weed species, F.spiralis, Ascophyllum, F.vesiculosus and F.serratus and the outcrops of rocks below the main rock platform did support F.serratus although it did not extend below MLWS. There were no laminarians.

The fauna of this site was very diverse, the presence of a boulder "reef" and the position of the site relative to the Estuary increased the number of marine species present.

2.3.3 SAWDERN

Grid reference : SM 888032

Aspect : SSW facing

Ballantine scale : 6-7

This was the most sheltered site chosen. It had dense algal beds, ranging from Pelvetia at high shore to laminarians at low water. The Ascophyllum beds were luxuriant and covered large areas of the shore. At low water there were substantial stands of F.serratus. This site is in the shadow of Milford Haven Oil Refinery and the only access was via a private road. Therefore it was an excellent site to use for field experiments.

The fauna at Sawdern was extremely diverse, being totally marine in origin.

GENERAL SUMMARY

The sites can be described as showing a cline of variation from the extremely sheltered shores (e.g. Sawdern) to moderately exposed shores (e.g. Porlock). The other shores fell between these two extremes. Their exposure is not easily defined from the traditional Ballantine scale which requires a variety of marine species to be present to calculate and is therefore inappropriate in an Estuary situation. The site at Aust, for example, although being relatively sheltered to wave action is subject to heavy tidal scour and reduced salinities. As such it could be regarded as being moderately exposed. The sites can be regarded as varying from "exposed" at Aust, Porlock; "exposed to sheltered" at Blue Anchor, Sully and Porthcawl to "sheltered" at Sawdern on an "exposure" scale judged from a combination of physical and biological factors. These exposure categories are only relative, as none of the sites are "exposed" sensu Ballantine (1961).

3. THE TAXONOMY OF THE FLAT PERIWINKLE GROUP

3.1 INTRODUCTION

The taxonomy of the flat periwinkle group has been the subject of much debate. Before 1966 Littorina obtusata was considered to be the sole species in this group. This classification was based on the work of Colman (1932) who showed the great variety in shell morphs to represent a geographical cline of the species. This work confirmed the earlier suggestions of Dautzenberg and Fischer (1914) who had concluded that the flat periwinkles all belonged to the same species and that certain morphs, for example the British form, should be allocated subspecific rank, in this case the subspecies or variety Littorina littoralis. Dautzenberg and Fischer also noted a smaller "minima" morph of the flat periwinkle which Sacchi (1961) referred to as a dwarf form of the species.

The elevation of this dwarf form to specific status as Littorina mariae by Sacchi and Rastelli (1966) was based not only on its smaller size when compared with L.obtusata but also on soft-body morphological features, principally the shape of the penis (see Sacchi and Rastelli 1966, and Goodwin and Fish 1977). Since this division there has been little doubt that L.obtusata and L.mariae do represent two species (for review see Raffaelli 1979). Evidence that substantiates their specific status concerns their ecology (Goodwin 1975; Goodwin and Fish 1977; Reimchen 1974); sexual dimorphism (Sacchi 1969a; Reimchen 1974; Goodwin 1975) and internal female anatomy (Goodwin and Fish 1977). The species have also been separated on a genetic basis, by

gel electrophoretic treatments (Wilkins and O'Regan 1980; Morris 1979; Warmoes 1986), and also on a biochemical basis (Reimchen 1974).

Despite this seeming wealth of data the field identification of these two species remains difficult. Goodwin and Fish (1977) have provided diagrams for the identification of the adults and juveniles by shell morphology. Many workers have found this guide misleading. Nielsen (1980) recorded that Danish material could not readily be identified using these criteria, and Watson (1983) opted not to classify juveniles from his Scottish sites due to the difficulty of identifying small specimens. Reimchen (1974) proposed that the sculpturing of the periostracum was a useful diagnostic character, but few authors have commented on this.

L.mariae exhibits morphological variation in a similar way to L.obtusata, and this has led to taxonomic confusion concerning the specific status of the morphological forms. Reimchen (1974 and 1981) recorded the presence of a dwarf form of L.mariae which differed slightly from the normal form in shell shape, penis morphology and shell sculpturing. These two forms also showed microhabitat separation and intermediate morphological forms were found in microhabitats considered to be intermediate between the habitats occupied by the two principal morphs. Reimchen (1982) believed that environmental selection such as predation by Carcinus maenus may be responsible for the variation between forms and proposed an informal taxonomic separation of the dwarf and large forms of L.mariae.

S.Smith also recorded a smaller form of L.mariae in the Uists (Smith 1978). This was a lagoonal animal termed "L.mariae beensis" (Fretter and Graham 1980). Nielsen (1980) noted a similar shell variety of L.mariae in Denmark which was a smaller, high-spired brackish-water variation of its larger, flat saline relative. The possibility of a second species of L.mariae has therefore received some support, but still remains unresolved. Recently the nomenclature of the species, L.mariae, has also been questioned. S.Smith (1982) suggested that the correct name for L.mariae is actually Littorina fabalis. This was based on a plate from Turton's collection (Turton 1825). If this suggestion is correct, L.fabalis is a senior synonym of L.mariae. Whilst drawing attention to the confusion over "L.mariae/fabalis" Smith also suggested the possible inclusion of other morphological forms of L.obtusata (e.g. L.aestuarii and L.palliata) as sub-species in the "flat periwinkle complex".

Electrophoretic studies by Moyse, Thorpe and Al Hamadini (1982) have shown L.obtusata and the morphologically similar L.aestuari not to differ genetically and a similar investigation has revealed L.mariae and L.mariae beensis also to be similar (S.Smith pers com). Smith now considers these morphological varieties to represent "ecomorphs" of L.obtusata and L.mariae. More recently, work by Warmoes (1986) described L.palliata as a northern form of L.obtusata.

In summary it is considered that in the flat periwinkle group there are two definite species - L.obtusata and L.mariae. There is some evidence to

suggest a number of sub-species or indeed species in a "L.mariae complex". The reproductive mode of these species which lay their eggs on their host alga species, and from which the young crawl out with no dispersal stage (Goodwin 1974), involves very little gene exchange between populations at isolated sites. The tendency for local morphological variation to be maintained is therefore very strong. On an evolutionary time scale this may result in speciation if geographic isolation is rigid, but in the present context the immediate result is a large variance of morphological forms about the mean types of the species L.obtusata and L.mariae.

In order to clarify this situation in the study area a detailed biometric survey was carried out to investigate the morph forms present in the Severn Estuary and to elucidate the exact nature of the species present.

3.2 MATERIALS AND METHODS

3.2.1 SAMPLE PROCEDURE

Collections were made at a number of sites along the Severn Estuary and at a marine site, Sawdern, in West Wales. The aim was to collect over 200 winkles of each "species". This was not always possible due to the scarcity of L.mariae at certain sites and its absence from Aust. The collections were made over the entire vertical range of the beach. Only adult winkles were collected, the thickening of the aperture lip being used as an indication of maturity (after Reimchen 1974, Goodwin 1975).

In the laboratory the winkles were killed by brief immersion in boiling water. This also induced muscle relaxation and consequently improved fixation of the material (Goodwin and Fish 1977). For this purpose 10% formalin was used, the winkles being transferred to 70% alcohol prior to investigation. The investigation can be divided into two main parts; firstly the investigation of the external "shell" features and secondly the investigation of the internal "soft body" features.

3.2.2 SHELL FEATURES

The shells of the winkles were all scored for colour (using the scheme of Dautzenberg and Fischer (1914) as revised by Reimchen 1974). Shell irregularities were seen to be of two sorts; either crack repair marks, such as those due to crab damage (see Reimchen 1982) or malformation of growth at the lip resulting in a ridge being formed. Consequently the irregular shell forms were scored as showing "crack" or "lip" damage. Most of the

irregular shell forms could be assigned to either of these categories. The shell shape of the winkles was measured using the parameters "a", "b" and "c" of Goodwin and Fish (1977) (after Colman 1932). These measurements were made to the nearest 0.05mm using vernier calipers.

3.2.3 SOFT BODY FEATURES

Once the shell had been scored, the animal was removed from the shell either by simply digging it out or by cracking the shell. The sex of the winkle was then determined. If the winkle was female then the ovipositor was examined for the presence or absence of pigmentation (Goodwin and Fish 1977, Nielsen 1980). If the specimen was male then the penis was dissected off the animal and examined separately. The number of adhesive glands and their arrangement was noted, and then the penis was drawn using a camera lucida. The tracing obtained was measured using a digitizing light pen and, once calibrated, length of the glandular part and length of the tip were determined.

This procedure was adopted for 100 animals of each sex from each site for the biometric survey as this was considered to be a statistically valid sample. As the population densities of L.mariae were very sparse in the Severn Estuary, sufficient numbers for analysis could only be obtained for Porlock and Sawdern.

3.3 RESULTS

3.3.1 L.obtusata

COLOUR MORPHS

Table 3.1 shows the results for the survey of L.obtusata shell colour, damage, sex ratios and ovipositor pigmentation at the six study sites. For all the sites, except Porlock, the predominant colour morph was olivacea. At these sites olivacea made up over 94% of the population. The second most common morph was reticulata (maximum = 6%) and other morphs found were citrina, fusca and aurantia. At Porlock the predominant morph was reticulata which accounted for over 95% of the population sampled. There was no noticeable difference between the sexes in the colour morphs found. All the differences were slight and showed no trend, both sexes always having the same dominant colour morphs.

OVIPOSITOR PIGMENTATION

Nearly all the female L.obtusata examined had pigmented ovipositors. All the females at Aust and Sully had pigmented ovipositors. At the other sites the maximum proportion of unpigmented ovipositors was 5% (at Sawdern).

SEX RATIO

The sex ratios for the six sites are shown in Table 3.1 and the results of a Chi-square test used to compare the sites are shown in Table 3.2. The initial Chi-square values denote whether the observed values vary significantly from an expected sex ratio of 1:1 (or in this case 100:100). For all the sites except Porthcawl the variations from this expected ratio were not significant,

Table 3.1
Colour morphs, ovipositor pigmentation, sex ratio and shell damage for L.obtusata at all the sites investigated.

SITE	SEX	COLOUR MORPHS	OVIPOSITOR PIGMENTATION	SEX RATIO	DAMAGE (%) CRACK	LIP	TOTAL
AUST							
	M	100=O	/	85	24	32	48
	F	98=O,1=C,1=A	100%	100	28	43	60
	TOTAL	198=O,1=C,1=A					108
SULLY							
	M	100=O	/	78	50	68	83
	F	98=O,2=R	100%	100	48	77	86
	TOTAL	198=O,2=R					169
BLUE ANCHOR							
	M	99=O,1=R	/	83	60	39	75
	F	100=O	97%	100	63	29	76
	TOTAL	199=O,1=R					151
PORTHCAWL							
	M	94=O,6=R	/	70	57	56	78
	F	95=O,5=R	95%	100	68	59	83
	TOTAL	189=O,11=R					161
PORLOCK							
	M	98=R,2=O	/	86	21	62	68
	F	96=R,3=O,1=C	99%	100	18	73	78
	TOTAL	194=R,5=O,1=C					146
SAWDERN							
	M	96=O,2=R,1=F,1=A	/	75	48	59	80
	F	98=O,2=R	95%	100	45	61	78
	TOTAL	194=O,4=R,1=A/F					158
GRAND TOTAL							
	M		/	79.5	43.2	52.7	
	F		97.7%	100	45	57	
	TOTAL						

KEY
M : Male
F : Female
COLOUR MORPHS: O = olivacea; C = citrina; R = reticulata; A = aurantia; F = fusca
TOTAL DAMAGE : Sum of all shells with some form of damage
CRACK : Damage caused by the shell cracking
LIP : Damage caused by growth fluctuations

Table 3.2
Chi-Square analysis to test whether there is any deviation between the sites from a sex ratio of 1:1.

SITES	DEGREES OF FREEDOM	CHI-SQUARE VALUE	SIGNIFICANCE
AUST	1	1.22	N.S.
SULLY	1	2.72	N.S.
BLUE ANCHOR	1	1.58	N.S.
PORTHCAWL	1	5.29	*
PORLOCK	1	1.05	N.S.
SAWDERN	1	3.57	N.S.
SUM OF 6 CHI-SQUARES	6	15.43	*
POOLED CHI-SQUARES	1	14.05	*
HETEROGENEITY	5	1.38	N.S.

KEY
* = significant deviation from a 1:1 sex ratio
N.S. = 1:1 ratio not disproved.

although for all the sites females were more numerous than males. Porthcawl showed a significant deviation ($P<0.05\%$) from the expected ratio of 100:100, again in favour of the females.

From this simple Chi-square test it could be concluded that all the sites except Porthcawl had populations with a 1:1 sex ratio. This investigation can, however, be refined by looking at accumulated Chi-square values, the Sum of the Chi-square values, which often holds more information than individual Chi-square values (such as those for the six separate sites, see Snedecor 1956). This technique gave a significant result which suggested that the combination of all the sites did not conform to a 1:1 sex ratio. A second refinement is that of pooling the Chi-square values. This method examines the six sites as coming from one large sample of a population. This also gave a significant Chi-square value and suggested that, for the species L.obtusata, the hypothesis that the sex ratio is 1:1 can be rejected. These methods can be further extrapolated to measure the inconsistency of the deviations of the sample ratios from the hypothetical 1:1 ratio- this is known as the Heterogeneity value of the sample. Using this method the value given was very small and non-significant, which suggested very little random variation and a pronounced consistency of oscillation around the 1:1 ratio.

In conclusion the results from the Sum of the Chi-square suggested that the population's ratios deviated from 1:1 with no distinction between excess or deficit. The significant Pooled Chi-square result suggested that

there was a predominant tendency towards deviations with a common sign (ie. towards the female sex). The non significant Chi-square for Heterogeneity emphasised the previous result by showing the absence of normal variation around the ratio 1:1; ie. the variation was all in one direction and that was towards an increase in the female sex. There was a tendency, therefore, for L.obtusata to have populations with a sex bias towards females; sufficient to result in the total sex ratio for the 6 sites varying significantly from the expected 1:1 ratio.

SHELL DAMAGE

It can be seen in Table 3.1 that there was a difference in the amount of damage received at the various sites but this did not seem to vary between the sexes at the respective sites. Table 3.3 shows the results of a Chi-square test to investigate whether there was any difference in the damage received by males or females. The null hypothesis was that there was no difference between the sexes for susceptibility to shell damage. This hypothesis was not disproved as none of the sites showed any difference in damage received between the sexes. The Summed value of the Chi-square test was also non significant. Consequently the null hypothesis that the sexes showed no differences in the amount of shell damage they received cannot be rejected.

As there was no difference between the sexes in the amount of damage received the pooled values for males and females were used to investigate the differences in damage received at the various sites. Table 3.4 shows the results for a Chi-square test to investigate whether there was any

Table 3.3
Chi-Square analysis to test whether there is any difference between the sexes in the damage received for the sites studied.

SITES	DEGREES OF FREEDOM	CHI-SQUARE VALUE	SIGNIFICANCE
AUST	1	2.9	N.S.
SULLY	1	0.34	N.S.
BLUE ANCHOR	1	0.37	N.S.
PORTHCAWL	1	0.796	N.S.
PORLOCK	1	2.54	N.S.
SAWDERN	1	0.12	N.S.
SUM OF 6 CHI-SQUARES	6	7.07	N.S.

KEY
N.S. = no significant differences between the sexes in the amount of damage received.

Table 3.4
Chi-Square analysis to test whether there is any difference in amount of shell damage received by L.obtusata at the sites studied.

SITES	DEGREES OF FREEDOM	CHI-SQUARE VALUE	
AUST	1	43.79	
SULLY	1	10.68	
BLUE ANCHOR	1	0.12	
PORTHCAWL	1	3.86	
PORLOCK	1	0.21	
SAWDERN	1	2.21	
GRAND TOTAL	5	60.87	* * *

RANK ORDER
SULLY > PORTHCAWL > SAWDERN > BLUE ANCHOR > PORLOCK > AUST

KEY
* * * = significant at the 0.01 level, therefore the amount of damage received varies between the sites.

difference between the sites for the amount of damage received. These total values represent shells that either show crack OR lip (malformation) damage. Of the sample of 200 winkles, by calculation 75% would be expected to show some form of damage. The Chi-square value showed that there was a significant difference in the amount of damage received between sites. The sites can be ranked according to the amount of damage received and the order is given at the bottom of Table 3.4. Sully showed the highest amount of damage with over 75% of its sample being damaged. Porthcawl, Sawdern, Blue Anchor and Porlock are grouped together; all showed damage rates very close to 75% of their samples, exhibiting very similar susceptibility to damage. Aust was the only site which received a very low amount of damage, slightly over 50% of the sample showing damage.

The types of damage were subdivided into the two categories "CRACK" and "LIP" damage and the results for similar Chi-square tests to investigate between site variation in the amount of damage received are presented in Table 3.5 for "crack" damage and Table 3.6 for "lip" damage. Both these Chi-square tests showed there to be a significant difference in the amount of damage received by the different sites. In the case of "crack" damage (Table 3.5) the calculated expected ratio was approximately 50:50 with a slight bias towards shells not being cracked. The sites could be divided into three groups. Firstly, Porthcawl and Blue Anchor, which had high numbers of cracked shells (approx 60%). Secondly came Sully and Sawdern, approx 50% of their shells having been cracked.

Table 3.5
Chi-Square analysis to test whether the amount of crack damage received varies between the sites for L.obtusata.

SITES	DEGREES OF FREEDOM	CHI-SQUARE VALUE
AUST	1	26.54
SULLY	1	1.97
BLUE ANCHOR	1	24.61
PORTHCAWL	1	27.52
PORLOCK	1	51.00
SAWDERN	1	0.48
GRAND TOTAL	5	132.1 * * *

RANK ORDER
PORTHCAWL = BLUE ANCHOR > SULLY = SAWDERN > AUST = PORLOCK

KEY
* * * = significant at the 0.01 level; there are differences in the amount of both types of damage received by the sites

Table 3.6
Chi-Square analysis to test whether the amount of lip damage received varies between the sites for L.obtusata.

SITES	DEGREES OF FREEDOM	CHI-SQUARE VALUE
AUST	1	24.26
SULLY	1	25.18
BLUE ANCHOR	1	34.58
PORTHCAWL	1	0.58
PORLOCK	1	12.95
SAWDERN	1	2.15
GRAND TOTAL	5	99.7 * * *

RANK ORDER
SULLY = PORLOCK = SAWDERN = PORTHCAWL >> AUST = BLUE ANCHOR

KEY
* * * = significant at the 0.01 level; there are differences in the amount of both types of damage received by the sites

Thirdly, Aust and Porlock, which had very low values, especially Porlock, only approx 25% of their populations having shells which had been cracked,

An expected ratio of 50 damaged to 50 undamaged was also calculated for the "lip" damage data (Table 3.6). As with the crack damage therewas a significant difference between the sites. For this damage the sites could not be divided into groups but showed a declining trend of damage in the order Sully/Porlock/Sawdern/Porthcawl/Aust/Blue Anchor. 75% of Sully's sample had lip damage and the Blue Anchor populations at the other end of the scale showed approx 40% of its sample as having been damaged.

The susceptibility of the winkles at the 6 sites to crack or lip damage seemed to be variable. There did not appear to be any relationship between the two types of damage. To investigate this the winkles, at each site, showing crack or lip damage were compared using Spearman's Rank Correlation. This gave a value of -0.314, which showed a slight discordance in the variables. The negative correlation suggested that as the susceptibility to crack damage of various sites increased so the susceptibility to lip damage decreased and vice versa. However this value was not significant and it was concluded that there was no correlation between the relative occurrence of the two damage types at the six sites.

PENIS DATA

Table 3.7 shows the results of the penis measurements for male L.obtusata. The Table shows that there was a considerable variation for all the parameters measured. The total length of the penis differed from a

Table 3.7
Mean and Standard deviations for penis measurements of male L.obtusata from all study sites. (n=100)

SITES	PARAMETER	MEAN±S.D.
AUST		
	Total length (mm)	5.45 ± 0.71
	No of glands (mm)	25.75 ± 6.45
	Gland length (mm)	4.02 ± 0.63
	Tip length (mm)	1.43 ± 0.33
	% Tip/gland	36.50 ± 10.8
SULLY		
	Total length (mm)	7.29 ± 0.94
	No of glands (mm)	36.60 ± 10.1
	Gland length (mm)	5.74 ± 1.02
	Tip length (mm)	1.54 ± 0.39
	% Tip/gland	28.90 ± 15.7
BLUE ANCHOR		
	Total length (mm)	6.85 ± 0.66
	No of glands (mm)	40.87 ± 7.87
	Gland length (mm)	5.51 ± 0.63
	Tip length (mm)	1.34 ± 0.26
	% Tip/gland	24.74 ± 5.48
PORTHCAWL		
	Total length (mm)	6.63 ± 0.72
	No of glands (mm)	36.52 ± 8.09
	Gland length (mm)	5.37 ± 0.70
	Tip length (mm)	1.26 ± 0.27
	% Tip/gland	23.90 ± 6.17
PORLOCK		
	Total length (mm)	6.13 ± 0.82
	No of glands (mm)	34.75 ± 7.99
	Gland length (mm)	4.87 ± 0.86
	Tip length (mm)	1.27 ± 0.30
	% Tip/gland	28.40 ± 21.7
SAWDERN		
	Total length (mm)	6.31 ± 0.62
	No of glands (mm)	35.97 ± 7.17
	Gland length (mm)	5.09 ± 0.60
	Tip length (mm)	1.22 ± 0.25
	% Tip/gland	24.44 ± 6.52

minimum of 5.4mm (at Aust) to a maximum of 7.3mm at Sully. The remaining sites had values around 6mm in the ascending order Porlock, Sawdern, Porthcawl and Blue Anchor. The number of adhesive glands on the penis varied from 25-40 per male between the sites. Blue Anchor was the site with the highest mean number, Aust was the site with the lowest. The other sites formed a close knit group with 34-37 glands per male. The values for the length of the glandular and tip regions for the different sites could not be so easily categorized. The values for the glandular length were quite similar, ranging from a mean minimum of 4.02mm at Aust to a mean maximum of 5.74mm at Sully. The other sites fell between this range in the ascending order Porlock, Sawdern, Porthcawl and Blue Anchor. The values for the length of the penis tip were again similar between the sites. Three sites had mean values between 1.22mm and 1.27mm (Sawdern, Porthcawl and Porlock) and these were the smallest found at all the sites. The other sites had mean lengths ranging from the maximum of 1.54mm at Sully, to Aust and then to Blue Anchor which most closely resembled the small group. The relative Tip to Gland percentages (T/G%) were very similar for all the sites. The range was between 24% to 37%; Aust had the highest percentage and Porthcawl the lowest. Percentage values for all the other sites fell between these extremes in the descending order Sully, Porlock, Blue Anchor and Sawdern.

The significance of these differences between sites was examined using One Way Analyses of Variance and then SNK Tests. The results for these tests are shown in Table 3.8. There were many significant differences between the

Table 3.8
F values for One Way Analyses of Variance, and SNK tests , to compare L.obtusata penis parameter values for the study sites.

PARAMETER	F VALUE	SIGNIFICANCE
Total length	71.39	* *
Aust < Porlock = Sawdern < Porthcawl < B.Anchor < Sully		
No of glands	39.16	* *
Aust < Porlock = Sawdern = Porthcawl = Sully < B.Anchor		
Gland length	65.84	* *
Aust < Porlock < Sawdern < Porthcawl = B.Anchor < Sully		
Tip length	16.76	* *
Sawdern = Porthcawl = Porlock = B.Anchor < Aust < Sully		
% Tip/gland	14.49	* *
Porthcawl = Sawdern = B.Anchor = Porlock = Sully < Aust		

* = P< 0.05 * * P< 0.01

sites. The results for the total penis length showed that the sites could be divided into four groups, all the sites showing different sized penes except Porlock and Sawdern which were similar. The number of glands was also significantly different between the sites. The SNK test showed that the sites could be divided broadly into three groups; Aust and Blue Anchor being two of the groups, at either end of the range, with the highest and lowest number of glands respectively. Mean values at these two sites were shown to be sufficiently different from the other sites to isolate them. Conversely all the other sites were sufficiently similar to warrant their grouping together in the middle of the range for the number of glands. All the other parameters measured also showed significant differences between the sites (all $P<0.01\%$). There was more variation between the sites for these parameters than for the number of glands. The mean values for the glandular length at the various sites were so dissimilar that the SNK test rejected any of the sites except Blue Anchor and Porthcawl as being similar. The sites were shown to be more similar for the size of the penis tip. At the top of the size range Aust and Sully were both isolated. The other sites were linked together as Blue Anchor, Porthcawl and Porlock which the SNK test considered to be similar; or Porthcawl, Porlock and Sawdern which were also given the same status by the SNK test. A similar division of the sites was seen in the T/G%. Aust was the only site isolated, at the top of the range, by the SNK test. The other sites were grouped as Sully, Blue Anchor, Porlock, Sawdern and as Blue Anchor, Porlock, Porthcawl and

Sawdern.

SHELL PARAMETERS

The values a, b and c for the shell parameters of both sexes are shown in Table 3.9. These results can be analyzed in a number of ways. Traditionally a large number of One Way Analyses of Variance would be carried out to investigate the null hypotheses that there was no difference between the sites or sexes for parameter a;b;c or separate combinations of the two. If the results were significant then the differences between the means would be further analyzed using one of the accepted tests for comparing mean values (e.g. S.N.K. Test, Scheffe's Test etc). This method of analysis would be very cumbersome and time consuming and would only present data concerning individual parameters; the relationships between these readings would not be considered.

A more robust technique is to carry out a Multivariate analysis which will consider all the variables and their relationships at the same time. The aim of this section was to elucidate whether there was any morphological difference in the winkle populations found at the different sites. Is it possible to distinguish between the populations using the shell parameters ? and if so can the shell parameters that are important for distinguishing between the sites be singled out ? The most appropriate technique to investigate these aims is a discriminant analysis. This procedure operates on grouped (i.e. the sites) individuals and produces a set of discriminant functions by which an individual can be allocated to one of the sites (see Janson and Sudberg 1983, Norusis 1983). The

Table 3.9
Mean and Standard deviations for parameters a, b and c for males and females L.obtusata from all study sites. (n=100)

SITES	PARAMETER	FEMALES	MALES
AUST			
	a	15.12 ± 0.66	15.09 ± 0.69
	b	10.43 ± 0.48	10.46 ± 0.57
	c	13.47 ± 0.67	13.57 ± 0.72
SULLY			
	a	17.02 ± 0.60	16.43 ± 0.77
	b	11.58 ± 0.58	11.36 ± 0.64
	c	14.95 ± 0.68	14.62 ± 0.71
BLUE ANCHOR			
	a	17.14 ± 0.69	16.69 ± 0.65
	b	12.12 ± 0.52	11.86 ± 0.55
	c	15.27 ± 0.76	15.02 ± 0.75
PORTHCAWL			
	a	16.82 ± 0.63	16.40 ± 0.68
	b	11.63 ± 0.62	11.34 ± 0.61
	c	14.89 ± 0.74	14.68 ± 0.75
PORLOCK			
	a	15.01 ± 0.51	14.72 ± 0.57
	b	10.23 ± 0.55	10.05 ± 0.57
	c	13.53 ± 0.63	13.26 ± 0.64
SAWDERN			
	a	16.33 ± 0.61	16.06 ± 0.59
	b	11.41 ± 0.61	11.19 ± 0.59
	c	14.88 ± 0.75	14.76 ± 0.76

programme used was the SPSSX programme DISCRIMINANT which also produces a canonical variate analysis. This analysis determines functions in terms of canonical variates which maximise the differences between the sites. These produce scattergrams which allow visual examination of the differences between the sites.

Before the data were analyzed they were transformed logarith mically (to base 10) to attain maximum separation of the groups (see Janson and Sundberg 1983). Janson and Sundberg further transformed their data to account for large winkles, thus biasing the analysis. In this study the data were not further transformed as it was important to include differences in the winkles' sizes between the sites in the analysis. Because this comparison hoped to investigate between-site differences, the varying sizes of the winkles between the sites were important variables. This method was valid as all the winkles were adults and would have reached a maximum size, which would be directly comparable between the sites.

MULTIVARIATE ANALYSIS FOR L.obtusata FEMALES.

The results for females correctly classified according to the discriminant analysis are presented in Table 3.10. These show a number of relationships between the sites. Overall 47% of the individuals could be correctly classified, which was greater than the 17% predicted by chance. Of these most of the sites had more than 50% of individuals from that site correctly identified, the only exception being Porthcawl which only had 14% of its winkles correctly assigned to the site. The misclassifications showed the close similarities in

Table 3.10
Percentage of L.obtusata females correctly assigned to their own site based on predictions made from canonical variates.

	PREDICTED GROUP MEMBERSHIP					
SITES	AUST	SULLY	B.ANCHOR	P'CAWL	PORLOCK	S'DERN
AUST	39%	6%	0%	4%	34%	17%
SULLY	12%	31%	23%	14%	2%	8%
B.ANCHOR	3%	14%	59%	10%	0%	21%
PORTHCAWL	12%	28%	30%	10%	0%	8%
PORLOCK	25%	0%	0%	0%	69%	5%
SAWDERN	17%	8%	21%	8%	5%	41%

Number correctly classified = 41.5%

Probability of correct classification = 16.67%

Table 3.11
Percentage of L.obtusata males correctly assigned to their own site based on predictions made from the canonical variates.

	PREDICTED GROUP MEMBERSHIP					
SITES	AUST	SULLY	B.ANCHOR	P'CAWL	PORLOCK	S'DERN
AUST	46%	4%	1%	0%	41%	8%
SULLY	0%	52%	23%	13%	0%	12%
B.ANCHOR	0%	19%	56%	7%	0%	18%
PORTHCAWL	5%	31%	29%	14%	1%	20%
PORLOCK	34%	0%	0%	1%	60%	5%
SAWDERN	8%	9%	16%	11%	5%	51%

Number correctly classified = 46.5%

Probability of correct classification = 16.67%

morphology between some of the sites. The relationships between the sites are displayed graphically in Figure 3.1. The combination of the misclassified individuals and the visual presentation of the canonical variates showed that Porlock and Aust were very similar morphclogically, often being misclassified with each other but rarely with the other sites. On the graph these sites were displaced to one side with comparatively little overlap with the other sites. All the other sites were grouped together and were often misclassified amongst themselves. This suggested that they were very similar morphologically.

MULTIVARIATE ANALYSIS FOR L.obtusata MALES.

The results for the classification of the male winkles are shown in Table 3.11 and graphically in Figure 3.2. Slightly less individuals were correctly assigned to their correct sites than for the females, although this was again above the value expected by chance. Otherwise the results were very similar to those obtained for the females. Aust and Porlock were again very similar and separated from the other sites. The other sites showed very similar morphologies, their distributions overlapping to a great extent and many individuals were misclassified between the groups.

For the multivariate analysis the eigen value is an expression of the variance of each discriminant function, and the cumulative percentage is the percentage of the variation explained by that function. The value of the coefficents is an indication of the influence of the character on the total variation of each function.

Tables 3.12 and 3.13 show the discriminant

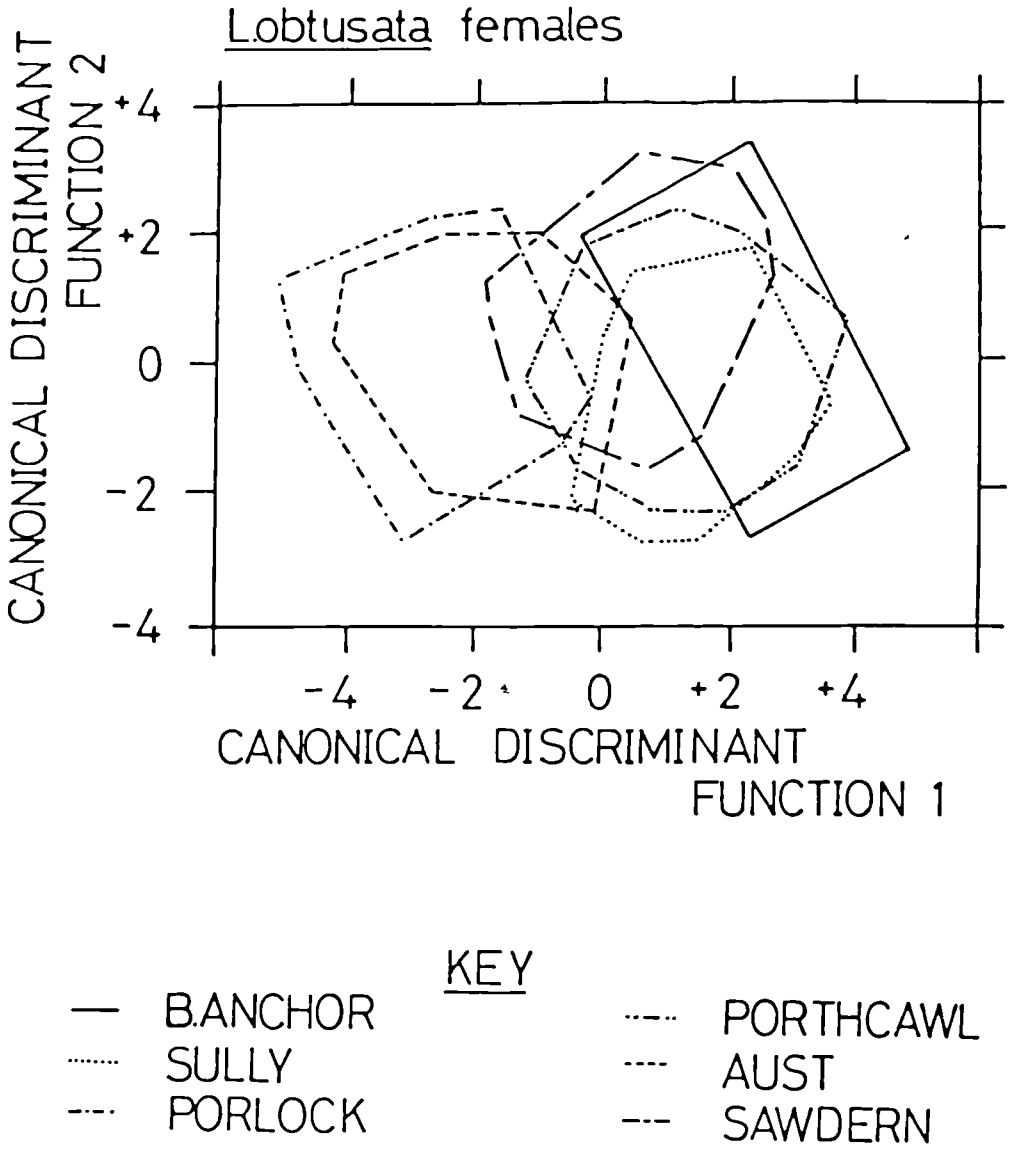


Figure 3.1
Projection of the first two canonical variables (estimated for shell measurements) for female L.obtusata from the six study sites.

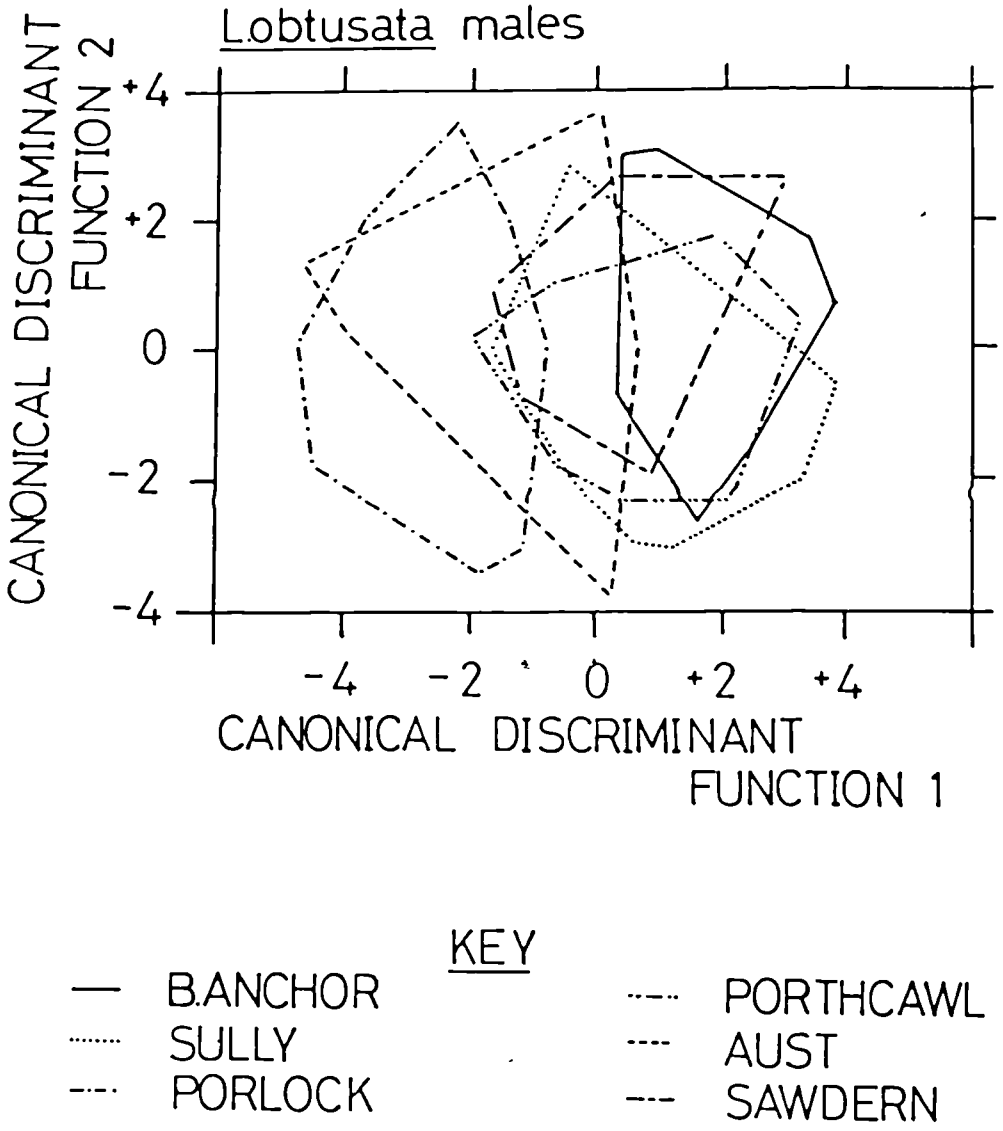


Figure 3.2
Projection of the first two canonical variables (estimated from shell measurements) for male L.obtusata from the six study sites.

Table 3.12
Discriminant functions and canonical coefficients for L.obtusata females at all the sites studied.

DISCRIMINANT FUNCTION	1	2	3
EIGEN VALUE	2.27254	0.16742	0.04172
CUMULATIVE PERCENTAGE	91.57	98.32	100.0
a	0.76712	-1.46634	0.05744
b	0.33026	0.86754	-0.88412
c	-0.01046	1.05606	0.96570

Table 3.13
Discriminant functions and canonical coefficients for L.obtusata males at all the sites studied.

DISCRIMINANT FUNCTION	1	2	3
EIGEN VALUE	1.44961	0.09896	0.03133
CUMULATIVE PERCENTAGE	91.75	98.02	100.0
a	0.48904	-1.66412	0.49785
b	0.45488	0.62565	-1.09886
c	0.19665	1.34364	0.63886

functions and canonical coefficents for L.obtusata males and females. These show that 92% of the variation between the sites was explained by the first discriminant function which was shell size a. This was most clearly seen for the females, the male values for a and b were very similar. The second function accounted for a further 6% of the variation and this again was accounted for by parameter a. The remaining 2% of the variation was accounted for by parameter c in the females and b in the males. The most important separating variable for both sexes was, therefore, shell size a.

3.3.2 L.mariae

Table 3.14 shows the results for shell colour, damage, sex ratio and ovipositor pigmentation of L.mariae used in this investigation.

COLOUR MORPHS

As for L.obtusata, the sites studied for L.mariae were dominated by a single colour morph. At Porlock the colour morph was reticulata, which was also the colour morph predominating in the L.obtusata population at that site. The L.mariae population at Sawdern were predominantly citrina in colour, althought some reticulata (light) were found. This was in direct contrast to L.obtusata at this site which were mostly olivacea, and provided a useful initial separation of the two species. At other sites in the Estuary where L.mariae was found the species displayed the reticulata colour morph, except at Flatholm where both citrina and reticulata morphs were found.

Table 3.14
Colour morphs, ovipositor pigmentation, sex ratio and shell damage for L.mariae at all the sites investigated.

SITE	SEX	COLOUR MORPHS	OVIPOSITOR PIGMENTATION	SEX RATIO	DAMAGE (%) CRACK	LIP	TOTAL
PORLOCK							
	M	80=R	/	80	26.4	52.9	69
	F	100=R	61%	100	31	67	75
	TOTAL	180=R					144
SAWDERN							
	M	42=C	/	42	40	36	62
	F	98=C,2=R	0%	100	65	32	74
	TOTAL	140=C,2=R					136
GRAND TOTAL							
	M		/	61	33.2	44.5	
	F		30.5%	100	48	49.5	
	TOTAL						

KEY
M : Male
F : Female
COLOUR MORPHS: C = citrina; R = reticulata;
TOTAL DAMAGE : Sum of all shells with some form of damage
CRACK : Damage caused by the shell cracking
LIP : Damage caused by growth fluctuations

Table 3.15
Chi-Square analysis to test whether there is any deviation between the sites from a sex ratio of 1:1 for the populations of L.mariae studied.

SITES	DEGREES OF FREEDOM	CHI-SQUARE VALUE	SIGNIFICANCE
PORLOCK	1	2.22	N.S.
SAWDERN	1	23.7	* * *

KEY
* * * = significant deviation from a 1:1 sex ratio at the 0.01 level
N.S. = 1:1 ratio not disproved.

OVIPOSITOR PIGMENTATION

None of the females at Sawdern had pigmentation on their ovipositors. At Porlock, however, over half of the female population had pigment somewhere on the ovipositor.

SEX RATIO

The sex ratios at the two sites were tested for deviation from a 1:1 ratio, and the results of the Chi-square test are shown in Table 3.15. This showed that although the population at Porlock appeared to be biased towards females,it did not deviate significantly from the 1:1 ratio. The population at Sawdern, however, was significantly biased towards females. The result is highly significant and would greatly weight any further Chi-square analysis so this was not attempted.

SHELL DAMAGE

Table 3.16 shows the result of a Chi-square to test whether there was any difference between the sexes in the amount of total damage received at the sites. Neither site showed a significant difference between the sexes. As a result of this lack of difference between the sexes the male and female results were combined for the subsequent analyses. These investigated whether there was any difference between Porlock and Sawdern in the amount of damage they received. Damage was further subdivided to investigate "crack" and "lip" damage. The results for these Chi-square Tests are shown in Tables 3.17, 3.18 and 3.19. These showed that there was no difference in the total amount of damage received at the two sites, but there were significant differences in the type of damage recorded. Sawdern had significantly greater crack damage

Table 3.16
Chi-Square analysis to test whether there is any difference between the sexes in the damage received for the sites studied.

SITES	DEGREES OF FREEDOM	CHI-SQUARE VALUE	SIGNIFICANCE
PORLOCK	1	0.86	N.S.
SAWDERN	1	2.08	N.S.

KEY
N.S. = no significant differences between the sexes in the amount of damage received.

Table 3.17
Chi-Square analysis to test whether there is any difference in amount of shell damage received by L.mariae at the sites studied.

SITES	DEGREES OF FREEDOM	CHI-SQUARE VALUE	
PORLOCK	1	0.051	
SAWDERN	1	0.049	
GRAND TOTAL	2	0.100	N.S.

KEY
N.S. = the winkles at the two sites receive a similar amount of damage

Table 3.18
Chi-Square analysis to test whether the amount of crack damage received varies between the sites for L.mariae.

SITES	DEGREES OF FREEDOM	CHI-SQUARE VALUE	
PORLOCK	1	15.00	
SAWDERN	1	15.76	
GRAND TOTAL	2	30.76	* * *

KEY
* * * = significant at the 0.01 level; there are differences in the amount of both types of damage received by the sites

Table 3.19
Chi-Square analysis to test whether the amount of lip damage received varies between the sites for L.mariae.

SITES	DEGREES OF FREEDOM	CHI-SQUARE VALUE	
PORLOCK	1	10.42	
SAWDERN	1	13.77	
GRAND TOT	2	24.19	* * *

KEY
* * * = significant at the 0.01 level; there are differences in the amount of both types of damage received by the sites

(Table 3.18) and Porlock had significantly greater lip damage (Table 3.19).

PENIS DATA

Table 3.20 shows the results of the penis measurements for L.mariae. The table shows little variation between the two sites; the penis sizes being smaller than those of L.obtusata and having a larger tip/gland ratio as would be expected from the species descriptions. Mean values at the two sites were compared using T tests and the results are shown in Table 3.21. These show that the L.mariae populations at Sawdern had larger penes than the population at Porlock. As a result the length of the tip and glandular area were also larger at Sawdern. The ratio of tip/gland length and the number of glands were not significantly different between the sites, showing the penis to be relatively similar in form but simply larger at Sawdern than Porlock.

SHELL PARAMETERS

The values for parameters a, b and c are shown in Table 3.22. As discussed for L.obtusata these were analyzed using Multivariate techniques. Over 50% of the males and females of L.mariae were correctly classified as shown in Table 3.23 and illustrated in Figure 3.3. The major difference in morphology was between the males from Sawdern and the other individuals. The other sexes and sites were very similar, grouped together on the scatter-plot and often being misclassified. The males from Sawdern, however, were slightly separated by the canonical functions and were only misclassified in 14% of the individuals.

Table 3.20
Mean and Standard deviations for penis measurements of male L.mariae from all study sites.

SITES	PARAMETER	MEAN±S.D.
PORLOCK (n=87)	Total length (mm)	4.13 ± 0.63
	No of glands (mm)	11.29 ± 2.28
	Gland length (mm)	2.61 ± 0.47
	Tip length (mm)	1.52 ± 0.35
	% Tip/gland	59.77 ± 17.09
SAWDERN (n=42)	Total length (mm)	4.47 ± 0.53
	No of glands (mm)	10.67 ± 1.46
	Gland length (mm)	2.78 ± 0.36
	Tip length (mm)	1.69 ± 0.35
	% Tip/gland	61.57 ± 14.99

Table 3.21
T values for T-Tests to compare L.mariae penis parameter values for the study sites.

PARAMETER	T VALUE	SIGNIFICANCE
Total length	3.28	* * *
No of glands	1.87	N.S.
Gland length	-2.28	*
Tip length	-2.64	* *
% Tip/gland	-0.61	N.S.

KEY
* = P< 0.05 * * P< 0.01 * * * P< 0.001

Table 3.22
Mean and Standard deviations for parameters a, b and c for males and females L.mariae from Porlock and Sawdern.

SITES	PARAMETER	FEMALES	MALES
PORLOCK		n=100	n=87
	a	11.25 ± 0.92	10.56 ± 0.89
	b	8.40 ± 0.63	7.83 ± 0.57
	c	10.02 ± 0.88	9.41 ± 0.85
SAWDERN		n=100	n=42
	a	10.18 ± 0.95	8.47 ± 0.78
	b	7.69 ± 0.62	6.31 ± 0.63
	c	8.98 ± 0.82	7.47 ± 0.80

Table 3.23
Percentage of L.mariae males and females correctly assigned to their own site based on on predictions made from the canonical variates.

	PREDICTED GROUP MEMBERSHIP			
SITES	PORLOCK		SAWDERN	
	females	males	females	males
PORLOCK				
females	70%	15%	14%	1%
males	32%	39%	24%	5%
SAWDERN				
females	21%	18%	50%	11%
males	0%	0%	14%	86%

Number correctly classified = 57.8%

Probability of correct classification = 25.00%

Table 3.24
Discriminant functions and canonical coefficients for L.mariae males and females at all the sites studied.

DISCRIMINANT FUNCTION	1	2	3
EIGEN VALUE	1.20196	0.04103	0.00006
CUMULATIVE PERCENTAGE	96.69	99.99	100.0
a	0.05356	0.34489	-0.00349
b	0.80340	-1.59825	0.29757
c	0.17641	1.45363	-0.07444

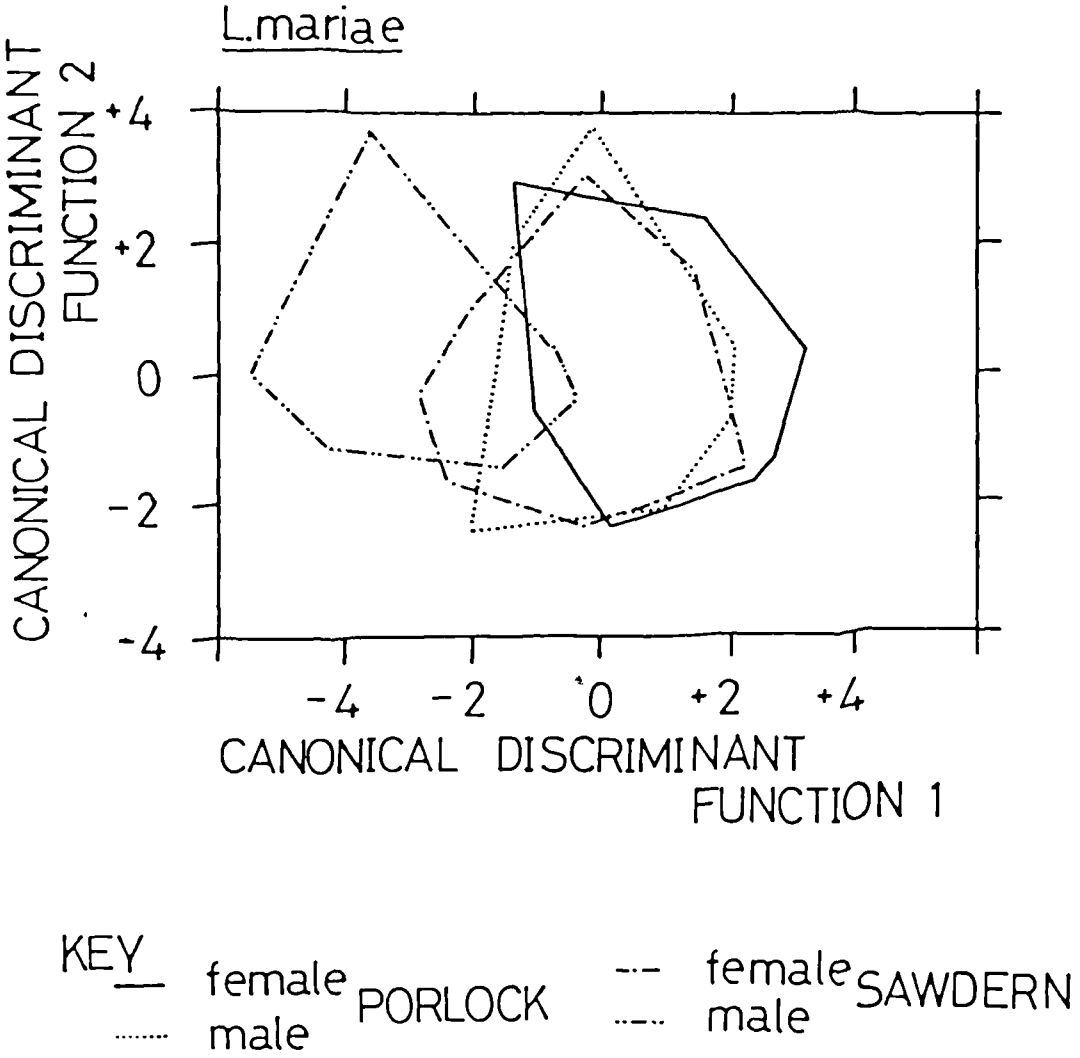


Figure 3.3
Projection of the first two canonical variables (estimated from shell measurements) for male and female L.mariae.

The discriminant function, eigen values and canonical coefficients for L.mariae are shown in Table 3.24. These show that 97% of the variation was explained by differences in parameter b, aperture size, as was the remaining 3% of variation. This parameter explained all the variation between the sites and sexes for L.mariae.

3:4 DISCUSSION

COLOUR MORPHS

The predominant morph of L.obtusata found at all the sheltered sites was olivacea. At the only marine exposed site, Porlock, the winkles were reticulated in colour morph. L.mariae also showed the reticulated morph at this site; whereas at Sawdern, a more sheltered site, the predominant morph was citrina. It is well documented that on sheltered shores L.obtusata has olivacea coloured shells and L.mariae has citrina coloured shells. On more exposed shores the predominant morph for both species becomes reticulata (Sacchi, 1966, 1967, 1969; Goodwin 1975; Goodwin and Fish 1977; Guiterman 1970; Smith 1976; Reimchen 1974 and Gratton 1969). Using this information some of the work completed before 1966 (and therefore based on one "species") can be assigned tentatively to either L.obtusata or L.mariae according to colour morph and collecting sites. The evolutionary selection of these colour morphs is complex and has been suggested as being due to predation selection (Reimchen 1974 and 1979; Smith 1976; Sacchi 1974).

OVIPOSITOR PIGMENTATION

Goodwin (1975) and Goodwin and Fish (1977) suggested that the lack of pigmentation on the ovipositor could be used as a diagnostic character to separate female L.mariae from L.obtusata. The results from this study agreed with this suggestion for the L.obtusata populations as at least 95% of each site's females had pigmented ovipositors. The separation also held true for L.mariae at Sawdern where all

the females had unpigmented ovipositors. At Porlock, however, approx. 60% of the females dissected had pigmented ovipositors, which did not allow separation between the two species as the female L.obtusata also had pigmented ovipositors. It is possible that this difference reflects a difference in scoring methods between this investigation and that of Goodwin who did not rigorously define the area scored in his study. In this study any pigment on the ovipositor (here defined as the folded, elevated area along the foot; see Fretter 1980 and Fretter and Graham 1962) was scored as being pigmented and this may be more rigorous than the procedure adopted by the previous authors. Nielsen (1980) also found difficulty in assigning individual females to the different species by this character and concluded that Danish specimens could not be divided on this basis.

SEX RATIOS

L.obtusata showed a significant trend towards a female bias in the sex ratios recorded in this study. A similar trend had also been noted by previous workers (Sacchi 1966, 1967, 1969; Goodwin 1975). Neither of these workers applied further statistical tests to the Chi-square analysis which might have confirmed the significance of the trend. In this study such analysis proved that the trend seen was significant. The trend seen for L.mariae, however, did not agree with earlier workers' observations. Both Sacchi (1969) and Goodwin (1975) recorded a general trend towards males in this species, whilst the present study suggested a heavy bias towards females, especially at Sawdern. This has been recorded previously, for what was

described as an exceptional population of L.mariae (Sacchi 1968). As all the previous workers have recorded a bias towards males it is possible that the conclusions from this study are anomalous and due to either a site-specific difference, or an error in the sampling procedure. It is possible that selection for adults with thickened shells when searching in the field resulted in an undersampling of the smaller male individuals, especially at Sawdern. If this is not the case then the sex ratio seen was a natural phenomenon and may reflect differential mortality or survival between the sexes (see Grahame 1977 and 1985 for similar work on Lacuna pallidula and L.vincta).

DAMAGE

For neither species was there a difference in the damage received by the sexes. There was, however, a difference between the populations from the different sites in the amount of damage received. The categories scored represent two different types of damage. The "crack" damage represents damage caused by cracking damage to the shells , such as crab attack or boulder crushing (Raffaelli 1978, Reimchen 1982). The "lip" damage has not been used by other workers. This type of damage is presumed to be the result of a growth arrest on the shell's development resulting in the formation of a band along the lip of the shell. The damage is, therefore, assumed to be the result of adverse physical conditions. The two types of damage are unrelated (as shown by the non-significant correlation coefficent) and represent the effects of different phenomena.

The amount of crack damage was highest for the most

sheltered shores (Sawdern, Porthcawl, Sully and Blue Anchor) as compared to the exposed shores (Porlock and Aust). This is presumably due to an increase in predation pressure by Carcinus maenas on sheltered shores (Crothers 1970; Raffaelli 1978; Reimchen 1982). Higher densities of crabs on sheltered shores would result in an increased encounter rate and corresponding large amount of damage at these sites. This explanation would account for the higher prevalence of crack damage at Sawdern as compared to Porlock for L.mariae. As the sites represent areas along a cline of environmental conditions this would explain the variation in the L.obtusata populations at the different sites. The increased selective pressure at sheltered shores has been suggested as driving morphological variation between winkles at sites along a gradient of exposure and tidal height (Guiterman 1970 and Reimchen 1974). This has been demonstrated on an evolutionary time scale by Seeley (1986) who showed that the morphology of L.obtusata had undergone change since the introduction of C.maenas to New England.

The incidence of lip damage was high at Sully for L.obtusata and for both L.mariae and L.obtusata populations at Porlock. As this form of damage is presumed to represent the effect of unfavourable conditions it may be assumed that sites with a high degree of this form of damage are environmentally unstable. These sites may be subject to fluctuating conditions which affect the winkles' growth. This damage may also represent the cessation of growth due to winter temperatures (similar to other molluscs: e.g cockles, Orton 1923). The exact nature of

this form of damage is unclear; but the high incidence, especially in the more dynamic sites, suggests that the growth of the species was often interrupted. This has previously been noted by Hollingworth (1980) who described L.obtusata as exhibiting a punctuated form of growth.

PENIS DATA

The dimensions of the penis were much more varied in L.obtusata than L.mariae. For L.obtusata all the measurements taken showed significant differences between the sites. This tended to follow differences in the body size of the winkles; Aust and Porlock having the smallest total length; Sully and Blue Anchor having the largest lengths. Aust was the only site significantly different from the other sites for the ratio of tip/gland length revealing that for most of the sites, despite the size difference, the proportions of the penes were similar. The same pattern was true for L.mariae; despite differences in size the relative proportions of the penes were similar.

SHELL PARAMETERS

The multivariate analysis for L.obtusata revealed that the populations from Aust and Porlock consisted of smaller individuals than those at the other sites, which were very similar morphologically. This was true for both males and females. Previous workers have shown that as the site becomes more "exposed" so L.obtusata becomes smaller in size and the converse is true for L.mariae (Sacchi 1969 a; Goodwin 1975; Goodwin and Fish 1977; Guiterman 1970; Reimchen 1974). This has been suggested as being due to increased selection pressure for an optimum body size at exposed sites (for attachment) and at sheltered sites

(improved protection from predators). The results from the present study agree with the trend for shell size varying along the exposure gradient as both species show separation of individuals between the most exposed (Porlock) and sheltered sites (Sawdern). Aust can also be included in the exposed category of shore as it is subject to high current speeds in the estuary, but is not exposed to wave action sensu stricto (see Little and Smith 1980).

The results for L.mariae showed some variation between the sites but mostly between the sexes at Sawdern. The males at Sawdern were much smaller than the females. This sexual dimorphism has been previously noted by Sacchi (1969b) and Goodwin and Fish (1977). The small size of these individuals suggested that they may be "dwarf" L.mariae as proposed by Reimchen (1981). The material was kindly examined by Professor Cain who confirmed that at both Sawdern and Porlock no dwarf L.mariae were found. The dwarf variety has not been found in this study; there did not appear to be any of the habitats typical of the dwarf L.mariae at the study sites. The present study was therefore concerned only with L.mariae sensu stricto. As a result of studying the plate in Turton's collection (Turton 1825) it was concluded that the shell shown was difficult to assign to a species with confidence. Due to the fact that the two species are primarily separated by soft-body morphological features, and shell form is extremely variable, it was decided that L.mariae was the correct name for the species and not L.fabalis (c f. Smith 1982, see also Fish and Sharp (1985) who described "fabalis" as being the young of L.obtusata/mariae).

GENERAL SUMMARY

For all the parameters studied, with the notable exception of female ovipositor colour, there were definite inter-specific differences between L.obtusata and L.mariae. These confirm the findings of earlier workers (Sacchi 1966 a, b, 1967, 1968, 1969, a, b, 1972, 1984; Goodwin 1975; Guiterman 1970; Reimchen 1974).

The most important effect on intra-specific variation between populations of each species seemed to be the environmental conditions of the sites in question. This study has shown, and numerous previous workers have commented on, the importance of the exposure gradient to the morphology of winkle species. This is thought to be mediated through differential selection pressures along the exposure gradient. Variations in morphology caused by the effects of exposure have been described for many winkle species: L.rudis (Raffaelli 1978); L.saxatilis (Janson 1982 a and b, Janson and Sundberg 1983); L.nigrolineata (Naylor and Begon 1982). The environment affects the selective forces which will act on the morphology of the species present. In the cases discussed above, these factors were thought to be primarily wave action and crab predation. For L.obtusata and L.mariae a number of other factors have also been suggested as being important.

The sites used in this study represent a number of different environments which affect the species in different ways. At exposed sites (such as Porlock) the algae are stunted and consist primarily of F.vesiculosus (often var. evesiculosus) and F.serratus. Boulders tend to

be prevalent and the substrate is often mobile and subject to intense wave action. The direct effect of wave action is probably the most important selective force acting on the winkle species, as predation pressure on these shores is low. Evidence to support this was provided by Guiterman (1970) who showed intra-specific differences between sites in the ability of L.obtusata to remain attached to algae under turbulent conditions.

On sheltered shores (such as Sawdern and Sully) predation is the important driving force and physical conditions are mild enough to allow large beds of Ascophyllum to grow. Predation from crabs has been shown to affect the morphology of L.obtusata selecting for larger, thicker shelled individuals (Seeley 1986); and has been proposed as being an important inter-specific selection factor accounting for the variation in morphology in L.obtusata and L.mariae (Reimchen 1982). Populations at either ends of these extremes of the exposure range will be under very different selection pressures: at the exposed shore to reach a size optimum to maintain a hold on the weed available, and on sheltered shores to reach a size that affords protection against predators. The results of the cline of these forces are seen in the variation in morphology of the populations of the two species studied at the sites between these extremes. The exact nature of the selective pressures are unknown and worthy of further study. The primary aim of this section was to ensure accurate field identification of L.obtusata and L.mariae; an investigation into morphological variation along an exposure gradient was outside the scope of this project.

4. VERTICAL ZONATION

4.1 INTRODUCTION

The rocky intertidal represents a vertical, dynamic environmental gradient between marine and terrestrial habitats. Along this gradient environmental conditions vary from fully marine to fully terrestrial. This transition is in proportion to the shore's topography relative to tidal fluctuations. The shore can be divided into broad bands using the coarse physical scale of tidal height. The upper part of the shore, which is uncovered for long periods during the tidal cycle, is termed the supra-littoral; the mid shore, which is submerged and emersed for approximately equal time periods, is called the eulittoral; and the lower shore, which is submerged for the longest period, is termed the sub littoral (for a detailed discussion see Lewis 1964). These zones reflect not only differences in periods of submersion:emersion but also differences in physical variables linked to this cycle. Physical conditions at the high shore are more variable, prolonged subjection to air increasing ranges of temperature, salinity, and other physical parameters. Lower shore areas have a much less variable environment being subjected to the buffering nature of submergence by the sea. (For detailed reviews of tidal levels and related physical conditions see Tait 1981, Lewis 1964 and Newell 1979.)

On a finer environmental scale there are many zones within these shore levels. These are delimited by micro-variations in the physical environment, representing

transitions between the broad tidal levels. Correspondingly intertidal species inhabit characteristic belts along this gradient. The zonation patterns of these species have been the subject of detailed study (Lewis 1964, Stephenson and Stephenson 1954). Early workers attributed the zonation patterns to the existence of these fine-scale environmental bands, the species occupying the zone which did not exceed their physiological tolerances. This was further expounded in the Critical Tidal Level hypothesis (Colman 1933) which proposed that species distributional boundaries coincided with points of inflexion along the emersion curve. Numerous authors have shown a correlation between species distribution and their physical tolerances (e.g. Wolcott 1973).

Recent work has cast doubt on this as the sole cause of zonation patterns (Underwood 1978b,1979; Connell 1972). It is thought that biological factors are at least as important, or even more important than physical factors in controlling zonation patterns. Interactions between species on the shore often result in the establishment of the upper/lower boundaries of the species zones. The zonation of macroalgae on the shore has been shown to be affected by physical factors (Hawkins and Hartnoll 1985; Little and Smith 1980) and by biological factors. In particular, these include the effect of interactions between weed species (Schonbeck and Norton 1978,1980; Johnson et al. 1974; Hawkins and Hartnoll 1985) and the effects of grazing by animal species. Grazing can limit the width of zone occupied by weed species (Hawkins and Hartnoll 1983; Connell 1972). Predation plays an important

role in controlling zonation patterns between animal species; such as the effect of Pisaster on mussels (Paine 1966) or Nucella on barnacles (Connell 1972). More subtle actions of biological factors influencing zonation have been documented for semi-exposed rocky shore communities (Petraitis 1987), entirely sedentary communities (Dayton 1971) and gastropods (Underwood 1979).

The zonation of mobile species, such as gastropods, is subject to the effects of behavioural stimuli. Whilst their zonation is governed by the same rules as those affecting sessile species, their methods of attaining/maintaining the correct zone are a result of behavioural movements either towards a beneficial stimulus or away from harmful stimuli (see Newell 1959; Wolcott 1973; Underwood 1977, 1979). The exact zonation patterns of mobile species are therefore often more complex than those of sessile species whose boundaries are fixed.

Present theory suggests that the zone occupied by a species is that in which it is able to perform optimally in that environment. Extension either above or below this zone brings the species into contact with other species , which are also zoned at their height of optimal performance. The "price" of this specialization for optimal performance on a narrow band within an environmental gradient is that the extending species is less well adapted than the other and cannot outcompete its neighbours (see J.L.Menge 1975 for details). It is the pressure of competition between species for resources along this intertidal gradient that has induced extreme specialization and results in zonation patterns. In

formalised niche terms, attempted extension of a species along this gradient from its realized niche to its potential niche (which is already occupied by other species) will involve competition with, and subsequent exclusion by, superior competitors in their own realized niches.

The zone occupied by a species along this dynamic environmental gradient is therefore a function of evolutionary selection for niche specialization. It is only within these specific niche dimensions that the species can perform optimally to the exclusion of other species. In this chapter the distribution of the flat periwinkles along this vertical gradient of dimensional heterogeneity is investigated, in order to elucidate the specific conditions under which the respective species have become specialized. This is combined with an investigation into the relationship between the winkles and their host algae. As the entire life histories of the winkles are spent on fucoid algae the niche dimensions of L.obtusata and L.mariae will be dependent on the host algae.

4.2 MATERIALS AND METHODS

4.2.1 VERTICAL TRANSECT

To investigate the vertical distribution of the winkle species along the shore fixed-point vertical transects were set up at the five Severn Estuary sites and Sawdern. This involved surveying the beach with a dumpy level and marking each metre drop in the gradient of the beach. The points were marked by drilling holes in the rocks, using a battery powered hammer drill, and bolting numbered stainless steel discs to the substrate. As a result the vertical axis of the beach was marked with a point at each metre drop in height.

At these sites the population of flat periwinkles was sampled using a 50x50cm quadrat. The number of quadrats chosen to be sampled at each site was 10, based on the results of a preliminary study. This showed that 10 quadrats gave a sample with an Index of Precision (Elliott 1977) greater than 90%. As most ecological surveys tolerate an error of 20% a sample size of 10 quadrats was considered robust enough to allow for variation in density and spatial distribution of the winkle populations. The 10 quadrats were positioned using a random number table at all the sites where the substrate was sufficently homogeneous to give a satisfactory replication of tidal height and weed cover. The quadrats were placed in a horizontal fashion, in a band, from the fixed point so that they would all be at the same relative height. The use of 10 replicate samples in such a band allowed for an investigation into horizontal distribution of the two species and also covered

a large area of shore, thus avoiding simple pseudo-replication (Hurlbert 1984).

In each quadrat the percentage cover of weed was scored using a double strung 100 point quadrat (Jones et al 1980). The weed was then systematically searched until no more winkles were found. To do this "tru-touch" medical gloves were worn as small winkles (those less than 2.5mm) often clung to the surface tension developed on the gloves. All damaged air-bladders were searched for juveniles (see Reimchen 1974, Goodwin 1975, Guiterman 1970). The number, colour and species of the winkles found was noted and all the winkles were measured using vernier calipers to an accuracy of 0.05mm.

4.2.2 RELATIONSHIP WITH ALGAE

The results from the vertical transect gave a coarse measure of the relationship between the winkles and their host algal species. To further investigate this relationship a study of the faecal material of the winkles was undertaken to elucidate what the winkles actually ate. This technique has been used by many other workers (Moore 1931, 1932; Kitting 1980;) and is considered to give an unbiased representation of what material is ingested (Nicotri 1977).

Faeces from animals in four different treatments were removed for analysis. These treatments were those used during the caging experiment (Chapter 6) and were L.obtusata and L.mariae on both Ascophyllum and F.serratus. Faeces were removed from five winkles of each treatment and the sample was divided into two: the first for macro-algal analysis and the second for micro-algal analysis.

For the macro-algal analysis the faeces were simply ground up , dehydrated and mounted in glycerine. The abundance of macro-algal cells was scored following the method of Jones (1968) as modified by Tsuda and Randall (1971). All the treatments were scored "blind" to ensure that there was no bias to the results (Gould 1981). The cells scored were compared with scrapes from macro-algae to ensure that they represented ingested algal tissue.

The remaining faeces were also ground up and underwent a cleaning process for diatoms using the Potassium Permanganate Method (Hasle 1987). Slides so prepared were examined for diatoms and the species found were noted. The nature of the preparation did not allow any quantitative measurements to be made between the treatments and so only qualitative results were obtained from this part of the investigation.

4.3 RESULTS

4:3.1 POPULATION DISTRIBUTION

VERTICAL ZONATION

Tables 4.1-4.6 show a summary of the results for the vertical height transects undertaken at the six sites. The values in the tables are means for 10 replicate quadrats at each height. Figure 4.1 gives histograms to show the distribution of the two species along the vertical gradient of the sites. It can be seen that L.obtusata reached a peak of density at mid-shore and decreased in abundance to either side of this. This general pattern was shown most clearly at Aust, Sully, Porthcawl and Sawdern, the sites with the largest winkle populations. All the sites showed a truncation of the species' distribution at the upper end of the shore. The distribution pattern at this level appeared to be skewed. The results from Blue Anchor were anomalous probably because of sparse winkle populations and the scoring of many egg mass hatchings present at the time of sampling.

At the sites where L.mariae was present it was found at the bottom of the shore. There was some overlap between the ranges of the two species; but this overlap represented the extreme downward extension of L.obtusata and the extreme upward extension of L.mariae. On a presence/absence basis these histograms show a clear separation in shore level inhabited by the two species. The only site where this was not apparent was at Porlock where, because there are only 2 heights at which algae was present, the zonation pattern appeared constricted. The

Table 4.1
Mean and standard deviation of numbers of L.obtusata and L.mariae and percentage cover of algal species along the vertical gradient of Aust.

TIDAL HEIGHT		L.obtusata	L.mariae	F.sp	F.ves	A.nod	F.ser
HIGH	1	4.9±4.9	0.0±0.0	0.0	62.8	0.0	0.0
	2	3.1±1.7	0.0±0.0	0.0	70.8	0.0	10.3
	3	34.0±9.8	0.0±0.0	0.0	22.7	37.3	2.5
	4	18.3±6.8	0.0±0.0	0.0	0.6	66.4	8.3
	5	7.8±5.0	0.0±0.0	0.0	0.0	16.1	78.3
	6	6.5±3.1	0.0±0.0	0.0	0.0	8.1	90.2
LOW	7	2.2±2.4	0.0±0.0	0.0	0.1	0.0	89.0

Table 4.2
Mean and standard deviation of numbers of L.obtusata and L.mariae and percentage cover of algal species along the vertical gradient of Sully.

TIDAL HEIGHT		L.obtusata	L.mariae	F.sp	F.ves	A.nod	F.ser
HIGH	1	11.6±5.6	0.0±0.0	96.9	0.0	0.0	0.0
	2	21.1±6.8	0.0±0.0	0.0	2.0	91.6	3.8
	3	11.0±4.1	0.0±0.0	0.0	11.1	51.4	33.3
	4	13.4±5.9	0.0±0.0	0.0	12.0	0.7	84.5
	5	7.1±4.2	1.2±1.8	0.0	5.5	2.2	88.8
	6	1.5±2.0	2.6±1.4	0.0	0.5	0.0	82.1
	7	0.8±1.1	1.2±1.5	0.0	0.4	0.0	76.4
LOW	8	0.1±0.3	0.5±0.7	0.0	0.0	0.0	78.3

KEY
F.sp = F.spiralis; F.ves = F.vesiculosus;
A.nod = Ascophyllum nodosum; F.ser = F.serratus

Table 4.3
Mean and standard deviation of numbers of L.obtusata and L.mariae and percentage cover of algal species along the vertical gradient of Blue Anchor.

TIDAL HEIGHT		L.obtusata	L.mariae	F.sp	F.ves	A.nod	F.ser
HIGH	1	2.2±2.4	0.0±0.0	76.5	0.0	0.5	0.0
	2	5.0±2.6	0.0±0.0	0.0	60.9	8.0	2.8
	3	27.7±19.7	0.0±0.0	0.0	74.9	1.2	1.8
	4	6.4±3.9	0.0±0.0	0.0	36.0	0.0	26.6
	5	4.2±2.2	0.0±0.0	0.0	0.3	0.0	86.3
	6	8.0±5.8	0.0±0.0	0.0	0.0	0.0	62.6
LOW	7	0.2±0.4	1.0±1.0	0.0	0.0	0.0	85.9

Table 4.4
Mean and standard deviation of numbers of L.obtusata and L.mariae and percentage cover of algal species along the vertical gradient of Porthcawl.

TIDAL HEIGHT		L.obtusata	L.mariae	F.sp	F.ves	A.nod	F.ser
HIGH	1	8.6±4.1	0.0±0.0	87.8	0.0	1.7	0.0
	2	14.4±7.0	0.0±0.0	0.0	6.4	75.1	0.2
	3	6.8±2.9	0.0±0.0	0.0	66.4	5.3	13.8
	4	0.6±0.7	0.5±0.7	0.0	8.4	2.4	69.3
	5	0.5±0.7	0.5±0.7	0.0	0.4	0.0	91.5
LOW	6	0.7±0.8	0.3±0.5	0.0	0.2	0.0	91.6

KEY
F.sp = F.spiralis; F.ves = F.vesiculosus;
A.nod = Ascophyllum nodosum; F.ser = F.serratus

Table 4.5
Mean and standard deviation of numbers of L.obtusata and L.mariae and percentage cover of algal species along the vertical gradient of Porlock.

TIDAL HEIGHT		L.obtusata	L.mariae	F.sp	F.ves	A.nod	F.ser
MID	1	6.8±3.7	4.1±1.7	0.0	18.5	0.0	0.0
	2	0.1±0.3	2.2±2.5	0.0	14.8	0.0	20.5

Table 4.6
Mean and standard deviation of numbers of L.obtusata and L.mariae and percentage cover of algal species along the vertical gradient of Sawdern.

TIDAL HEIGHT		L.obtusata	L.mariae	F.sp	F.ves	A.nod	F.ser
HIGH	1	9.4±7.0	0.1±0.3	91.7	1.7	1.4	0.0
	2	58.3±8.4	0.2±0.4	0.0	4.7	95.2	0.0
	3	34.5±8.2	1.6±1.3	0.0	1.0	98.2	0.0
	4	18.0±7.6	1.8±2.0	0.0	3.8	95.4	0.1
LOW	5	0.4±0.7	18.1±7.8	0.0	0.0	0.0	91.2

KEY
F.sp = F.spiralis; F.ves = F.vesiculosus;
A.nod = Ascophyllum nodosum; F.ser = F.serratus

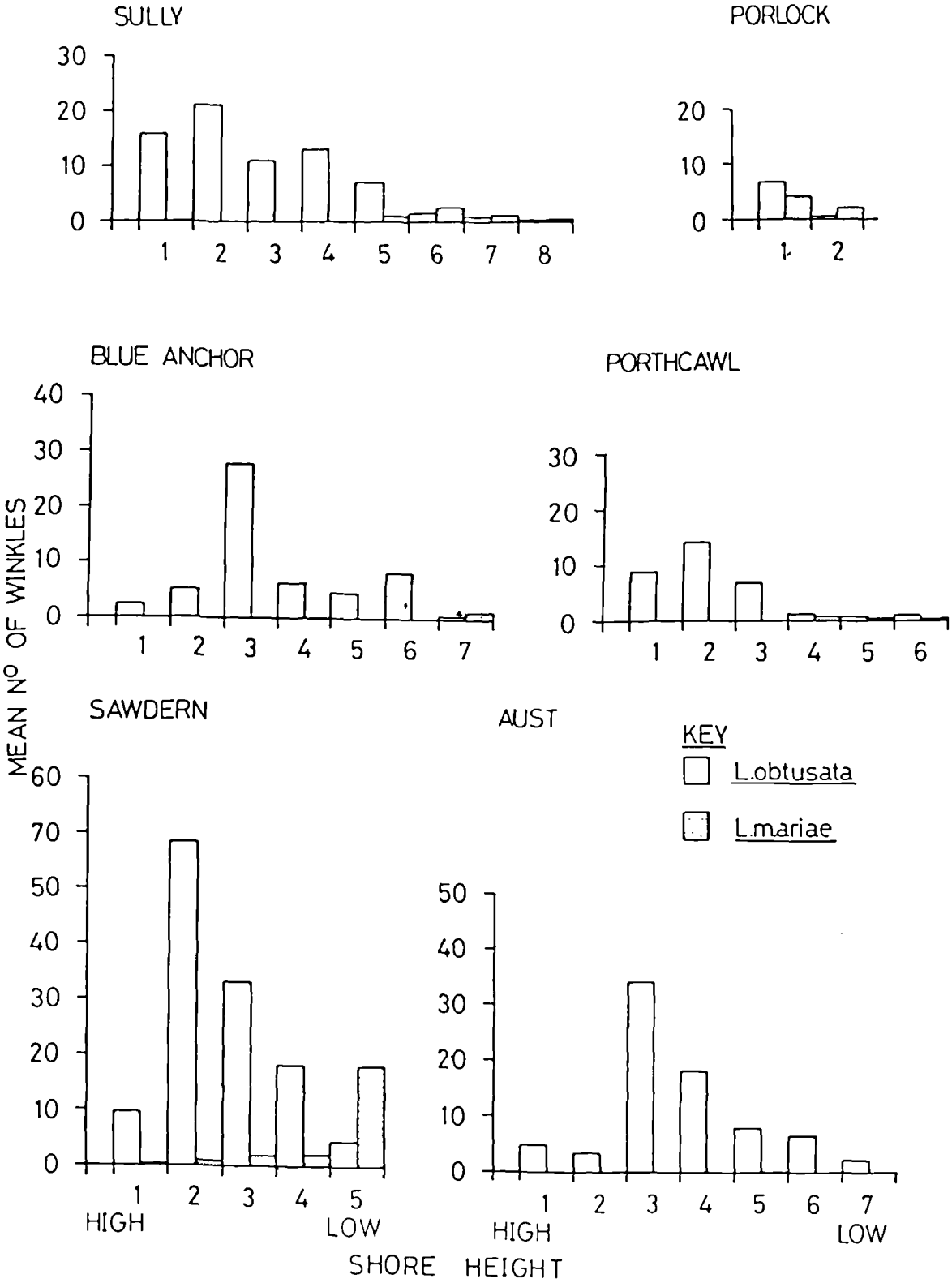


Figure 4.1
Vertical distribution of L.obtusata and L.mariae at one metre height intervals at the six study sites. On the horizontal axis number 1 represents the top shore site and the increasing numbers represent 1m drops down the shore.

other sites showed that L.obtusata inhabited the entire vertical range of the shore, whereas L.mariae only appeared at the bottom of the shore.

This trend in the distribution pattern of the winkles was examined using a Kruskal-Wallis test to investigate whether the mean number of winkles differed significantly down the beach. This was only done for L.obtusata as L.mariae's frequency was too low to validate such a test. The results for the test are given in Table 4.7 and show that for all the sites there was a significant difference in the number of L.obtusata at the different tidal heights. L.obtusata had a peak of distribution at mid shore, the density decreasing to either side of this peak. Due to the lack of substrate upshore the distribution in this direction was truncated. Downshore algal cover was not limiting but the population density gradually decreased in this direction.

The results for the distribution of L.mariae appear clear enough from the histograms. The species occured at low shore being recorded in the bottom sample heights.

HORIZONTAL ZONATION

As a result of sampling ten quadrats (effectively 10 sample units) at each height the dispersion of the populations on a horizontal scale could be calculated for the individual heights and also for the entire vertical range. This was done using the X2 test (Variance to Mean ratio) where the null hypothesis tests for deviation from a random distribution. Variations can be assigned to either contagious or regular distributions (Elliot 1977). Table 4.8 shows the results for these tests. In the case of

Table 4.7
Kruskal Wallis values to test the hypothesis that there is no differences in the number of winkles found at the different heights along the shore for the sites studied.

SITES	No of Heights	Chi-square Value	SIGNIFICANCE
AUST	7	23.86	* *
SULLY	8	63.79	* * *
BLUE ANCHOR	7	39.58	* * *
PORTHCAWL	6	45.67	* * *
PORLOCK	2	14.00	* * *
SAWDERN	5	44.32	* * *

KEY
* =P< 0.05; * * = P< 0.01; * * * = P< 0.001

Table 4.8
Dispersion Indices for L.obtusata at all the sites studied.

SITE	TIDAL HEIGHT	Chi Square	DISPERSION
AUST	1	44.28	Contagious
	2	8.69	Random
	3	25.5	Contagious
	4	22.87	Contagious
	5	28.85	Contagious
	6	13.31	Random
	7	22.59	Contagious
	TOTAL	889.4	Contagious
SULLY	1	24.33	Contagious
	2	19.55	Contagious
	3	13.48	Random
	4	23.46	Contagious
	5	22.68	Contagious
	6	24.24	Contagious
	7	14.63	Random
	8	9.00	Random
	TOTAL	619.76	Contagious
BLUE ANCHOR	1	24.38	Contagious
	2	12.38	Random
	3	125.93	Contagious
	4	21.32	Contagious
	5	10.37	Random
	6	37.51	Contagious
	7	7.99	Randomious
	TOTAL	1194.68	Contagious
PORTHCAWL	1	17.94	Random
	2	30.88	Contagious
	3	10.83	Random
	4	7.14	Random
	5	9.07	Random
	6	8.65	Random
	TOTAL	438.56	Contagious
PORLOCK	1	18.21	Random
	2	9.00	Random
	TOTAL	101.17	Contagious
SAWDERN	1	46.65	Contagious
	2	10.95	Random
	3	17.54	Random
	4	28.88	Contagious
	5	10.98	Random
	TOTAL	944.27	Contagious

Total number of heights = 35
number Contagious = 18
number random = 17
ALL Totals were Contagious

L.obtusata the results illustrate that at the individual heights the distributions of the winkles were equally split between random and contagious distributions. For a combination of all the heights at each shore L.obtusata was shown to have a contagious distribution. The results for L.mariae, Table 4.9, show that it appeared to be more randomly distributed than L.obtusata. The low numbers of L.mariae at all the sites, except Sawdern, made the validity of this inference suspect. The result for the bottom site at Sawdern (which had the highest number of L.mariae) showed a contagious distribution and is probably the most representative result for L.mariae.

SIZE DISTRIBUTION

One way Analyses of Variance were carried out on the values for winkle size at each height for L.obtusata to compare the size distribution of winkles along the vertical gradient. L.mariae was not present in sufficient numbers at enough sites to validate such a test. The hypothesis tested was that there was no difference between the size of winkles along the vertical gradient of the beach. Significant differences were further analyzed by SNK Tests and the results are shown in Table 4.10. These show that at all the sites except Sawdern there was a significant difference in winkle size between the heights. At Sawdern there was no significant difference in the size of winkles along the shore. There did not appear to be any pattern to this variation, although there was a slight trend for the large winkles to be found in the middle of the population's range. The SNK Tests confirmed this observation, the winkles at the edge of the species' range tending to be

Table 4.9
Dispersion Indices for L.mariae at all the sites studied.

SITE	TIDAL HEIGHT	Chi Square	DISPERSION
SULLY	5	22.97	Contagious
	6	7.08	Random
	7	16.43	Random
	8	9.07	Random
	TOTAL	67.80	Contagious
BLUE ANCHOR	7	8.02	Random
	TOTAL	8.02	Random
PORTHCAWL	4	9.07	Random
	5	9.07	Random
	6	6.91	Random
	TOTAL	26.40	Random
PORLOCK	1	6.57	Random
	2	25.36	Contagious
	TOTAL	31.90	Random
SAWDERN	1	9.22	Random
	2	7.94	Random
	3	9.07	Random
	4	19.80	Contagious
	5	30.25	Contagious
	TOTAL	35.60	Random

Table 4.10
One Way Analyses of Variance to test the hypothesis that there is no difference in winkle size along the vertical gradient of the shore at the sites studied.

SITE	SOURCE OF VARIATION	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARE	F
AUST	Among sites	6	55.44	9.24	5.34
	Within winkles	57	98.69	1.73	* *
	TOTAL	63	154.13		
SULLY	Among sites	6	555.51	92.58	14.25
	Within winkles	51	331.34	6.49	* *
	TOTAL	57	886.85		
BLUE ANC'R	Among sites	5	536.32	107.33	23.0
	Within winkles	48	223.94	4.66	* *
	TOTAL	53	760.46		
PORTH-CAWL	Among sites	5	299.98	59.99	9.54
	Within winkles	36	226.44	6.29	* *
	TOTAL	41	526.42		
SAW-DERN	Among sites	4	15.46	3.87	1.01
	Within winkles	38	145.20	3.83	NS
	TOTAL	42	160.69		

KEY
* * P < 0.01; NS = Non Significant

smaller than those at the middle. It should be noted that at some of the sites the lack of adequate replication of individuals may account for some of the variation noted, especially at the extremes of the species' distribution along the shore. It should also be emphasised that not all the SNK Tests showed the same trend.

4.3.2 RELATIONSHIP WITH ALGAE

Table 4.11 shows the results of Correlation coefficents calculated to investigate the relationship between the winkle species and their host alga species. These correlations were calculated for the combination of all the heights at each site. These show that L.obtusata was positively correlated at all the sites except Blue Anchor and Porlock with Ascophyllum nodosum, these correlations all being highly significant. L.mariae was positively, and again significantly, correlated with F.serratus at all the sites except Porlock. Both species were negatively correlated with the preferred algal host of the other species i.e. L.obtusata was negatively correlated witn F.serratus at all the sites; and the same was true for L.mariae and A.nodosum. These results are to be expected as there is an obvious relationship between the winkles and their host algal species.

The results for the faecal analysis are shown in Table 4.12. These showed a large difference between the treatments, especially between L.obtusata and L.mariae. At both mid and low shore L.obtusata had significantly more macro-algal tissue in the sample than L.mariae. There was also a large difference between L.obtusata treatments at mid and low shore. At mid shore there were a lot of

Table 4.11
Correlation coefficients between the winkle and algae species at the different sites.

SITES	F.sp	F.ves	A.nod	F.ser
AUST				
L.obtusata	/	.27 *	.51 ***	-4.1 ***
SULLY				
L.obtusata	.16 NS	.15 NS	.62 ***	-.56 ***
L.mariae	/	/	-2.9 ***	.39 ***
BLUE ANCHOR				
L.obtusata	-.19 NS	.56 **	-.33 NS	-2.5 *
L.mariae	/	/	-.09 NS	.39 ***
PORTHCAWL				
L.obtusata	.25 *	.17 NS	.67 ***	-7.5 ***
L.mariae	/	/	-.19 NS	.42 ***
PORLOCK				
L.obtusata	/	.38 NS	/	-.55 ***
L.mariae	/	.10 NS	/	-.19 NS
SAWDERN				
L.obtusata	-.35 ***	.25 NS	.71 ***	-.55 ***
L.mariae	/	/	-.51 ***	.89 ***

KEY
* $P < 0.05$; *** $P < 0.01$; NS = Not significant

Table 4.12
Macro-algae found in winkle faecal samples.

Each sample value represents a sweep of 5 areas for the presence of macro-algae. The score represents the number of points of intersection made by the eye-piece grid with a macro-algal cell.

	L.obtusata		L.mariae	
SAMPLE	MID	LOW	MID	LOW
1	8	13	0	3
2	12	6	4	7
3	11	23	1	6
4	24	15	4	8
5	46	44	8	4
6	8	14	1	10
TOTAL	119	115	18	38

The result of a Kruskal Wallis Test to compare the 4 samples gave a Chi-square value of 14.58, which is significant at the 0.01 level. Therefore the amount of macro-algae in the four samples was statistically different.

fragments of orange cell masses, possibly Ascophyllum reproductive conceptacles, on the slides. There was, however, little difference in the amount of epidermal and cortical cells in the L.obtusata faeces from different treatments. Many of the cells seen were fractured and empty of cell contents. Larger clumps of cells tended to be complete. At mid shore there was some Polysiphonia included in the sample. At low shore this was not the case, but there was much debris and many diatoms. Again, at this level, many of the cells were fractured and fragments of cell walls were found.

Fragments of cells were rarely found in the faeces of L.mariae. As can be seen from the Table it was only at low shore that any appreciable quantities of algal thallus tissue were found. At mid shore there were very few; there was ,however, some reproductive tissue of Ascophyllum found and a large clump of Ulva lactuca. There also appeared to be a large proportion of fragments and debris, and some microalgae were present. Microalgae, diatoms and debris were also recorded at low shore for L.mariae. In this treatment most of the macro-algal cells found were complete and few fractured cell walls were found. A number of cell clumps were found at this level. The debris found at this level, apart from the micro-algal component, seemed of a more inorganic nature than the debris at mid shore.

There was a large difference in the micro-algae found in the mid shore treatments (on Ascophyllum) and the low shore treatments (on F.serratus). Both L.obtusata and L.mariae appeared to have more diatom species in their faeces at low water, and also greater numbers of these

diatoms. The species found included Nitzschia sp; Navicula sp; Fragilaria sp; Diploneis sp; Acnanthes sp; Cocconeis sp; Amphora sp and other unidentified species. Unfortunately more detailed work on the micro-algal diet of the two species was outside the scope of this study. The only result that was ascertained was the increased amount of diatoms found in the faeces of both species at low shore as compared to mid shore.

In effect the results suggest that the difference in vertical zonation of the two winkle species may not be an abiotically enforced pattern due to tidal effects, but could be a biotic one enforced by the zonation patterns of both macro-algae and epiphytic micro-algae.

4.4 DISCUSSION

4.4.1 POPULATION DISTRIBUTION

VERTICAL ZONATION

Previous workers have noted a difference in the tidal height occupied by L.obtusata and L.mariae (Sacchi and Rastelli 1966, Sacchi 1969, Goodwin 1975, Bray 1974 and Reimchen 1974) but this separation has only recently been quantified (Watson and Norton 1987). The results from this study showed a distinct difference between the zonation of the two species. L.obtusata was found at all the heights examined on the shores. It reached a maximum density at mid-shore and decreased to either side of this. L.mariae's range, however, was far more restricted, being confined to the lowest heights sampled.

This represents a clear partitioning of the vertical gradient of the shore. There was some overlap between the ranges of the two species at mid to low-shore but this was slight and probably reflected individuals washed from their home ranges by the sea.

The vertical slope of the shore represents a gradient of physical factors associated with the transition from a marine to a terrestrial environment. The zonation of the winkle species on this gradient may be dictated by these physical factors. The emersion:immersion ratio indicates the extent of fluctuations in physical conditions which will be experienced at that height. At mid-shore, where L.obtusata is at its most dense, the species will experience an emersion:immersion ratio of approx 50:50, i.e it will be uncovered by the sea for approx 6 hours and

covered by the sea for 6 hours. This long exposure to air will result in large fluctuations in physical variables such as temperature and humidity. L.mariae living at low shore will experience less physiological stress as the low shore area is emersed for approx 2 hours per tidal cycle and so is not subject to such prolonged aerial influence. Living at mid shore means that L.obtusata will be exposed to a more variable physical environment than L.mariae at low shore -a more physically stable environment.

One of the most important variables for marine animals exposed for large periods of time is desiccation (Sacchi 1969). At mid shore, L.obtusata will experience greater desiccation stress than L.mariae at low shore. L.obtusata shows behavioural adaptations to counteract this problem. When the alga dries out, L.obtusata crawls into the centre of the weed mass and remains relatively dormant until emersed (Bray 1974, Sacchi 1963 -comparing different colour morphs (=L.obtusata/mariae) of "L.obtusata"). This represents a period of time when L.obtusata feeds less than when immersed, so desiccation will effectively limit L.obtusata's growth. Although L.obtusata will be under greater physiological stress at mid shore as compared to L.mariae at low shore, Sacchi (1969, 1972a and b) has shown L.obtusata to be more tolerant of desiccation than L.mariae. L.mariae is able to overcome this problem by living at low shore, and only being exposed for short periods. As a result L.mariae can actively browse during the entire tidal cycle.

Workers have investigated temperature tolerances in L.littoralis (L.obtusata subsp L.littoralis) but these

results are misleading due to the inadvertent inclusion of L.mariae in samples before its actual identification (see Daguzan 1976, Manigault 1932, Sacchi 1963 and 1966). Sacchi (1972a and b) has investigated temperature tolerances of the two species sensu stricto, and has again shown L.obtusata to be a more tolerant species than L.mariae being able to withstand greater ranges of temperature. Like the data for desiccation, these figures are based on laboratory work and may not reflect environmental differences (see Wolcott 1973 for discussion), but they do illustrate the relative difference between the two species.

There is no work based on the effect of other physical factors on L.obtusata and L.mariae. From the evidence given it could be suggested that the zonation of the two species can be explained by their physical tolerances. L.obtusata is the more tolerant species therefore inhabiting the majority of the shore, peaking in density at mid shore which is possibly its physiological optimum. L.mariae is more susceptible to desiccation stress and temperature fluctuations and so inhabits the more physically stable low-shore.

HORIZONTAL DISTRIBUTION

The two distribution patterns shown by the winkle species are contagious and random. That is the individuals are either associated together in clumps or are distributed randomly on the weed. Patterns such as this should be treated with care as the pattern shown by the winkles will be a reflection of numerous variables such as the lie of the algae after the tide has fallen and perhaps clumped

predation pressure. Any aggregated pattern may represent a hydrographic feature clumping the habitat and consequently the weed (for a discussion see Bray 1974). Therefore the distribution pattern in effect scores the distribution pattern of the algae if it is assumed that the number of winkles/unit weed is constant. This is an incorrect assumption as the original distribution pattern of the winkles will be aggregated in the form of egg masses. From these egg masses the young hatch and crawl, presumably with finite dispersal potential, unless under the control of the sea.

This influence of wave action on winkle populations results in their distribution being highly dynamic (Bray 1974, Guiterman 1970). When this effect is combined with algal drift (Ascophyllum growing over 3m and floating vertically at high water) the distribution pattern of the winkles must be extremely variable.

SIZE DISTRIBUTION

The same theory applies to the distribution of different-sized winkles along the vertical gradient of the beach. The significant differences between the heights at all the shores except Sawdern reflects this. There was a slight trend for the smallest winkles to be found at the extremes of the range for L.obtusata. This is, however, not consistent for all the sites and only significant in the cases of Sully and Aust. Other workers have shown the absence of any migration between shore levels (Hollingworth 1980). It is possible that the differences are due to sampling error, since Sawdern had the largest replication of individuals, and also had no difference in winkle size

along the shore.

There are a number of anomalies that can be explained, for example at Blue Anchor one of the mid shore heights had a number of egg mass hatchings and this will introduce a bias to the results. The timing of hatching will be variable at different sites and different shores. These will also be very localized and may be reflected by the results. The most probable explanation is mixing of the populations by random factors (as discussed for horizontal distribution).

4:4:2 ALGAL PREFERENCES

The zonation patterns of the two species was more complex than any simple reflection of physical conditions as they also closely correlated with the host species of algae. L.obtusata was strongly positively correlated with Ascophyllum and L.mariae is strongly postively correlated with F.serratus. This association between winkle and weed species has been noted by many authors. All have recorded L.obtusata as showing a preference for Ascophyllum /F.spiralis or F.vesiculosus and L.mariae for F.serratus (Sacchi 1969, 1972, Goodwin 1975, Bray 1974 and Reimchen 1974). Previous workers (that is before 1966) will possibly have included the two species under the same name and so earlier work has to be ignored or examined very carefully. Recent work has been consolidated and clarified by Watson (1983) who has investigated the relationship between the winkles and their host algae in great detail. Watson looked at the effect of algal exudates, sporelings and whole plant edibility , attractiveness and palatability on the winkles. His results showed that both species have

strong relationships with fucoid algae and they are attracted to their exudates and physical presence (Watson and Norton 1987).

The coarse diet analysis attempted in this study confirmed the results of other workers, showing that L.obtusata principally grazed Ascophyllum, actually eating the macro-algae, and L.mariae browsed micro-epiphytes off F.serratus. The exact mode of feeding of the two species has only recently been investigated. Previously the winkles were described as feeding/living on the algae. These observations were supported by a confusing number of preference experiments where the relative attraction of an alga species to "L.obtusata" was investigated (see Van Dongen 1956; Barkmann 1955 and Bakker 1959). These investigations were not only poorly devised but would have also included L.mariae with L.obtusata. The results from these were mostly inconclusive, but did show a preference of the flat winkles for fucoid algae (Bakker 1959; Van Dongen 1956).

When the two species were separated in 1966, there was still confusion over their diets. L.mariae was often referred to as feeding like L.obtusata (Fretter and Graham 1980), where L.obtusata was described as feeding on the host algae and encrusting diatoms. If this statement is true then the trophic dimensions of the niches of the two species would be identical. The only difference would be that they were spatially separated by inhabiting different belts (and hence zones) of weeds. Recent theory was still divided as to the exact mode of feeding employed by the two winkles. The main point of contention was whether

micro-algae or macro-algae were the more important food resource. J.L.Menge (1975) working on the New England coast of America believed that, in the case of L.obtusata, ephemeral algae were the most important constituent of winkle diet. She proposed this theory on the strength of personal observations (using SCUBA) of L.obtusata grazing, when only epiphytes were seen to be grazed off Ascophyllum, and also via experimental work. During laboratory experiments L.obtusata would not eat Ascophyllum and even in field cage experiments during the winter no record of grazing damage was found on Ascophyllum. During this same experiment, however, L.obtusata was found to eat Fucus distichus. This experiment was conducted during the "Fall" and Menge suggested that as the winkles grow little in the winter macroalgae are not a very important part of the diet with respect to the animal's growth. The presence of large amounts of ephemeral algae in Spring/Summer coinciding with maximal winkle growth was suggested as circumstantial evidence for the importance of micro-algae as a food source.

This is not considered to be true on British Coasts; although Reimchen (1974) did suggest, without any evidence, that epiphytes may be the primary food source of L.obtusata. Watson (1983) believed that both L.obtusata and L.mariae eat large amounts of macro-algae and disclaimed suggestions that this is incidentally taken in when browsing for micro-algae. He investigated the radula of both species and conducted numerous feeding trials. His results showed that both species are able, and preferred to excavate the thallus of perennial algae. Watson concluded

that L.obtusata and L.mariae were specialists, grazing on their host algae. He acknowledged the importance of micro-algae in the winkles' diet but suggested that this may be a more important resource for juvenile winkles and may be causal in separating the two species.

Many British workers agree that L.obtusata grazes on macroalgae (Galvin pers. com) and that the species leaves distinctive grazing marks on the thallus of Ascophyllum. These marks have been noted in New England by Petraitis (1987 and pers comm) who also believed that L.obtusata grazes the thallus of Ascophyllum. Similar indirect evidence was provided by Young (1975) who labelled F.serratus with Zn 65 and measured the transference of this isotope to L.obtusata as a result of grazing.

The results from this study, where large amounts of macro-algae were found in the faeces of L.obtusata at both mid and low shore, support the theory that L.obtusata is principally a macro-algal grazer and this is confirmed by the recent work of Watson and Norton (1987). This does not rule out the importance of micro-algae as a part of L.obtusata's diet, indeed, these may be very important to juveniles. The amount of micro-algae found in the faeces agrees with this, but as Kitting remarked (1980) any species grazing macro-algae will take in surface diatoms. The lack of large amounts of macro-algae in the faeces of L.mariae, coupled with the large amounts of diatoms at this level, points to micro-algae being a more important constituent of L.mariae's diet than that of L.obtusata. The reduced growth of L.mariae at mid shore (see Chapter 6) may be due to a limiting amount of micro-algae and an

inability to graze Ascophyllum. Watson (1983) and Watson and Norton (1987) have commented on the inability of the reduced buccal musculature of L.mariae, as compared to L.obtusata to graze Ascophyllum effectively.

It is unlikely that either species eats only macro- or micro-algae. The important difference is the amount that each contributes to the respective winkles' diet. This study and that of Watson and Norton (1987) have shown that macro-algae are more important as a resource to L.obtusata and micro-algae to L.mariae. This seems appropriate as Ascophyllum is a long-lived alga (Baardseth 1970, Cousens 1981) which has few epiphytes; whereas F.serratus has a large number of epiphytic species (Round 1984). As such this represents a trophic separation of the niches of the two species.

4.4.3 CONCLUSIONS

Attempting to separate algal zonation patterns and the gradient of physical variables on the shore as factors causing winkle zonation is difficult if not impossible from observation alone. Low-shore physical factors, for example, cannot be isolated as important limiting factors for L.mariae to the exclusion of the presence of its host algae F.serratus. As these are irrevocably linked (F.serratus being zoned at low shore), the argument becomes circular. The most acceptable conclusion is that the factors combine to influence the zoning patterns of the winkle species.

A major physical factor not previously mentioned but which affects the shore in general is wave action. The relative exposure of the shore to wave action dictates the

physical environment in which the shore organisms exist. The zonation patterns of the algae vary greatly with wave exposure, sheltered shores bearing large weed beds and exposed shores having very few macro-algae (see Lewis 1964 for detailed review). All the shores in this investigation were sheltered, varying between "very sheltered" and "sheltered to exposed" (Ballantine 1961). As these shores differed in their physical characteristics and weed zonation so the winkle distribution patterns varied. Other workers have noted an increased overlap of the two species' ranges on more exposed shores (Sacchi 1969, Sacchi and Rastelli 1966, Goodwin 1975, Reimchen 1974), this being associated with a decrease in the amount of weed cover (especially of Ascophyllum). At such relatively exposed shores the size difference between L.obtusata and L.mariae becomes less, possibly representing a similar selective force on both species (Goodwin 1975, Goodwin and Fish 1977). As shores become more exposed, L.obtusata (and its mid shore alga) become increasingly rare, but L.mariae remains as long as F.serratus is present. Some authors have actually commented on the surf-loving nature of L.mariae (Sacchi and Rastelli 1966, Sacchi 1969 and Fretter and Graham 1980).

Of the shores investigated in this project only two show a deviation in winkle zonation from that suggested. Both these shores, Blue Anchor and Porlock, are less sheltered than the other shores and neither has luxurious stands of Ascophyllum (Porlock has none). The zonation patterns on these shores may be influenced by wave action. At Porlock the constricted zonation patterns can be

assigned to increased exposure affecting algal distribution. Consequently there are no algae above mid shore, and only F.vesiculosus and F.serratus below mid shore. As a result the zonation of the two winkle species is greatly constricted and they show a high degree of overlap. It is also interesting that at this shore both species show the reticulated colour morph, which has been noted at exposed shores by other workers (Reimchen 1974, Goodwin 1975).

The physical tolerances of the two species can be seen as important parameters defining their niche dimensions. Following this theory it can be seen that L.obtusata has a much wider niche than L.mariae. It is more tolerant to both temperature and desiccation stress than L.mariae and therefore its range along the environmental gradient of the shore is greater than that of L.mariae. L.obtusata has a wider potential niche than L.mariae. This potential niche is modified to the realized niche of the species by other factors such as the distribution of the host algae. Therefore L.obtusata has an optimum distribution in the Ascophyllum zone (which is possibly its physiological optimum as well); and L.mariae is restricted to the F.serratus zone due to both biotic and abiotic limitations.

5. POPULATION STRUCTURE

5.1 INTRODUCTION

Numerous workers have attempted to investigated the life histories of the flat winkles. Most of this work has concentrated on L.obtusata (Guiterman 1970, Goodwin 1975, Reimchen 1974, Hollingworth 1981). Sampling such populations on sheltered shores has proved problematical. Various workers have used a number of different techniques in order to obtain a "representative" sample of the population. All of these involve collecting a number of winkles; either per unit time (Reimchen 1974, Goodwin 1975) or by weight of algae (Guiterman 1970, Wright 1976). These samples are then measured in the laboratory and size-frequency diagrams plotted of the populations. These histograms have been analyzed (Guiterman 1970, Goodwin 1978, Hollingworth 1981) by polymodal growth analysis using the methods of Harding (1949) and Cassie (1954).

The results of this work have been summarised by Hollingworth (1981) and described in detail by Goodwin (1978). Goodwin suggested that for most of the year L.obtusata's population shows a bimodal size frequency distribution. This is made up of a stable adult component and an actively growing juvenile component. This distribution becomes briefly trimodal due to the influx of very small winkles, a result of egg masses hatching (at Goodwin's site between May and June). At this time the previous year's juveniles are approaching adult size and merge with the stable adult component of the population, the overall population structure returning to being

bimodal.

Goodwin considered that the winkles hatching in May one year will leave the juvenile component of the population and reach maturity by October/December of the next year (a period of 18 months). This opinion is shared by Hollingworth (1981) who supported this theory with detailed work on L.obtusata's growth rates. Goodwin further stated that there is no evidence for any variation in growth rates at different shore levels, or any seasonal migration (as seen for L.littorea; Daguzan 1976; Smith and Newell 1955) in L.obtusata. The longevity of L.obtusata was considered to be approx 3+ years by Goodwin (1978). Investigations by other workers reached a similar conclusion (Guiterman 1970, Hollingworth 1981,). Daguzan (1976) suggested that the species lived up to 4 years. His work on the population structure and vertical distribution of L.obtusata agreed with Goodwin.

It appears, therefore, that the population dynamics of L.obtusata are well understood. There is some variation between workers' observations but most of these can be explained by environmental factors, such as micro-habitat variations, altering the speed or timing of the pattern described by Goodwin (1978). The population structure and associated dynamics of L.mariae are less well understood. Sacchi (1969) noted that the population was very unstable and fluctuated greatly in numbers. Apart from this casual field observation no one has looked at the population dynamics of L.mariae. It was towards a comparative study of the two species population dynamics that this section was devoted.

5.2 MATERIALS AND METHODS

A sampling regime similar to that used in Chapter 4 was adopted. All the sampling was conducted at Sawdern in West Wales. As previously described the shore was surveyed and marked via fixed bolts at every 1m difference in height. This gave 5 stations. At these stations 2 quadrats were sampled (see Chapter 4 for details of the technique) for winkles and algal cover. This gave a total of 10 quadrats over the entire shore, an area of 25,000cm squared. This sample size was based on the preliminary investigations carried out for the vertical height transects (see Chapter 4). The distribution of quadrats allowed any variation along the shore to be accounted for and resulted in an accurate sample of L.obtusata being obtained. All sampling was non-destructive and wholly carried out in the field.

In the case of L.mariae, which is restricted to the lower part of the shore, 10 quadrats were sampled at this level. These included the two fixed points used in the main transect. Two grids of 4 quadrats were also used which were located at the same level of the shore and marked by bolts.

Therefore the two species' populations were both sampled to the same degree. These samples were conducted every month for an entire year. The sample periods between the two species differed because the primary interest was initially in the population dynamics of L.mariae and the L.obtusata survey was included at a later date for comparative purposes. Unfortunately the data for the

L.obtusata sample for November are incomplete and therefore not included in this section.

5.3 RESULTS

5.3.1 L.obtusata

Figure 5.1 (a to k) shows the size frequency histograms for monthly samples of L.obtusata populations at Sawdern. This investigation was started in July 1986. All these histograms have a number of peaks of size class frequency which represent fluctuations in the population dynamics of L.obtusata.

In July there were two principal components to the population. Firstly there was a peak of recently hatched juveniles, below 4mm, and secondly a peak of adults, in the size range 14-17mm. Between these size ranges there was an irregular scatter of individuals. The histogram for August showed a similar pattern: The number of juveniles had decreased but they still accounted for the major proportion of the population. The second peak, representing the adults, was also in the same size range as for July and there was a similar scattering of individuals between these two peaks. There was a suggestion that the recently hatched juvenile peak was wider in August than July; and this trend was seen more clearly in September where this juvenile component of the population was seen to extend to include winkles up to 5-6mm. The number of newly hatched winkles had further decreased at this time of the year, less than 35 individuals being found below 2.5mm as compared to 45 being found in August. The number of adults had also dropped, although the peak is still obvious and in the same size range as the previous months. The frequency of individuals between these two principal size classes was

a)

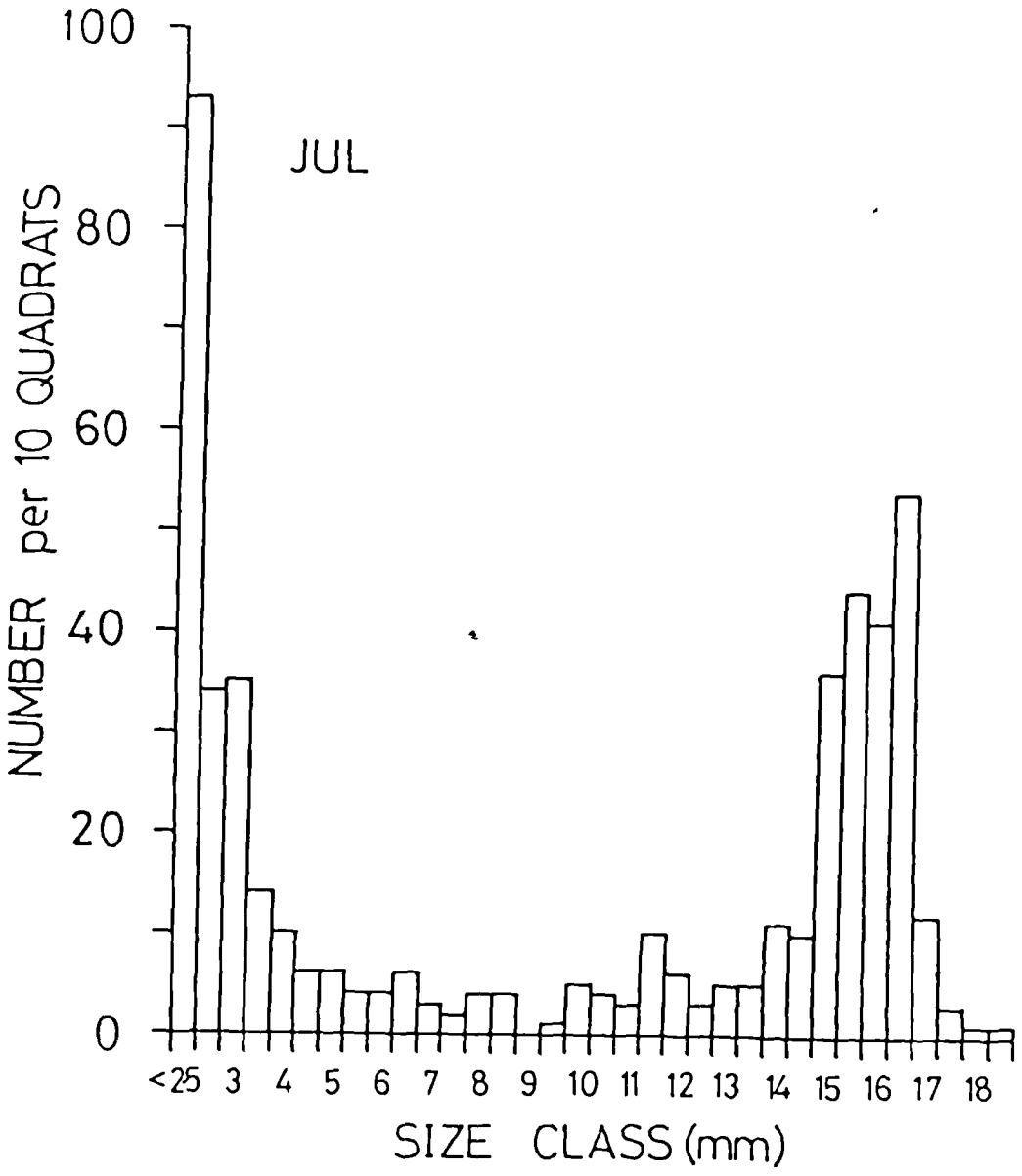
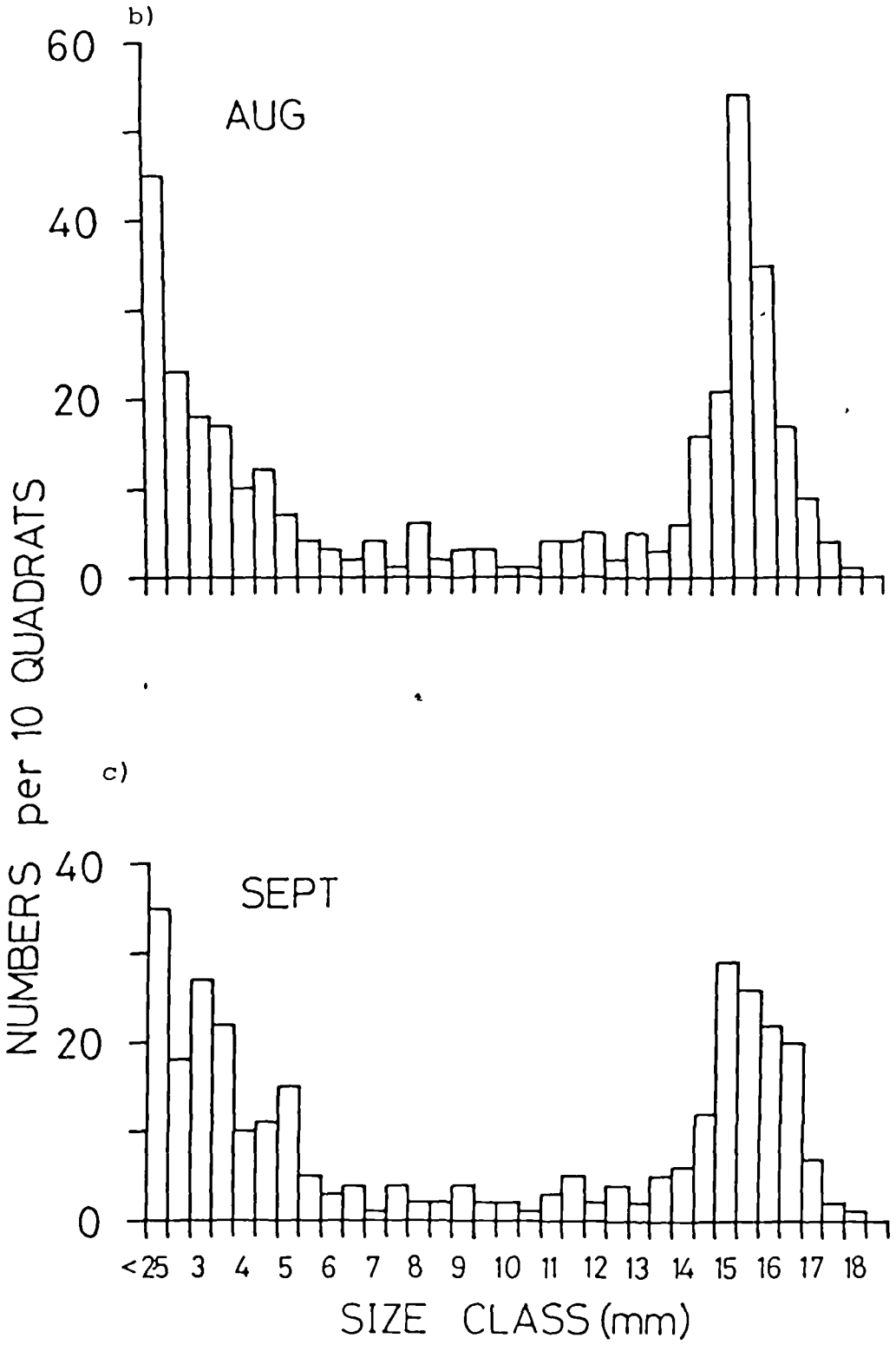
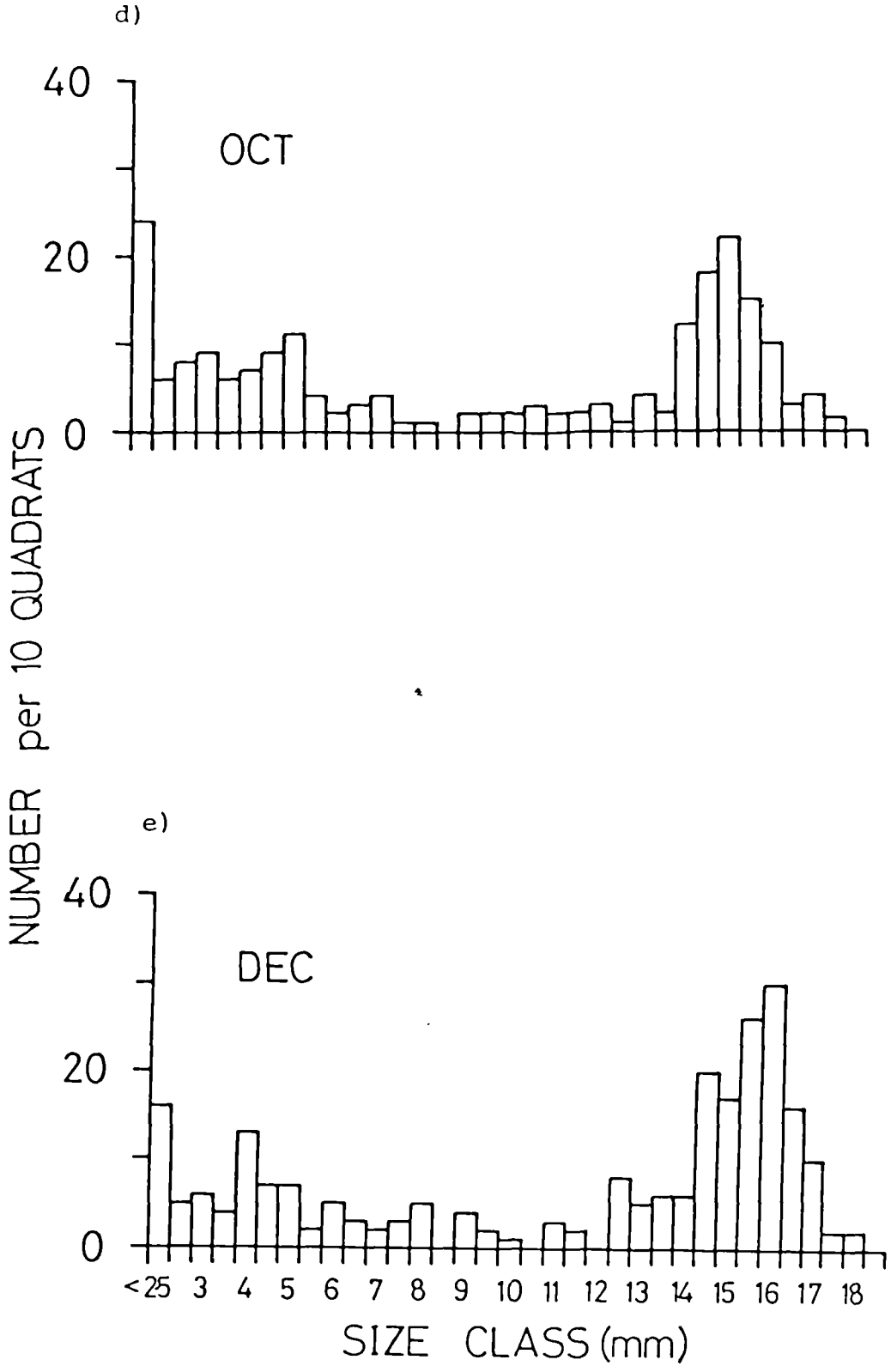


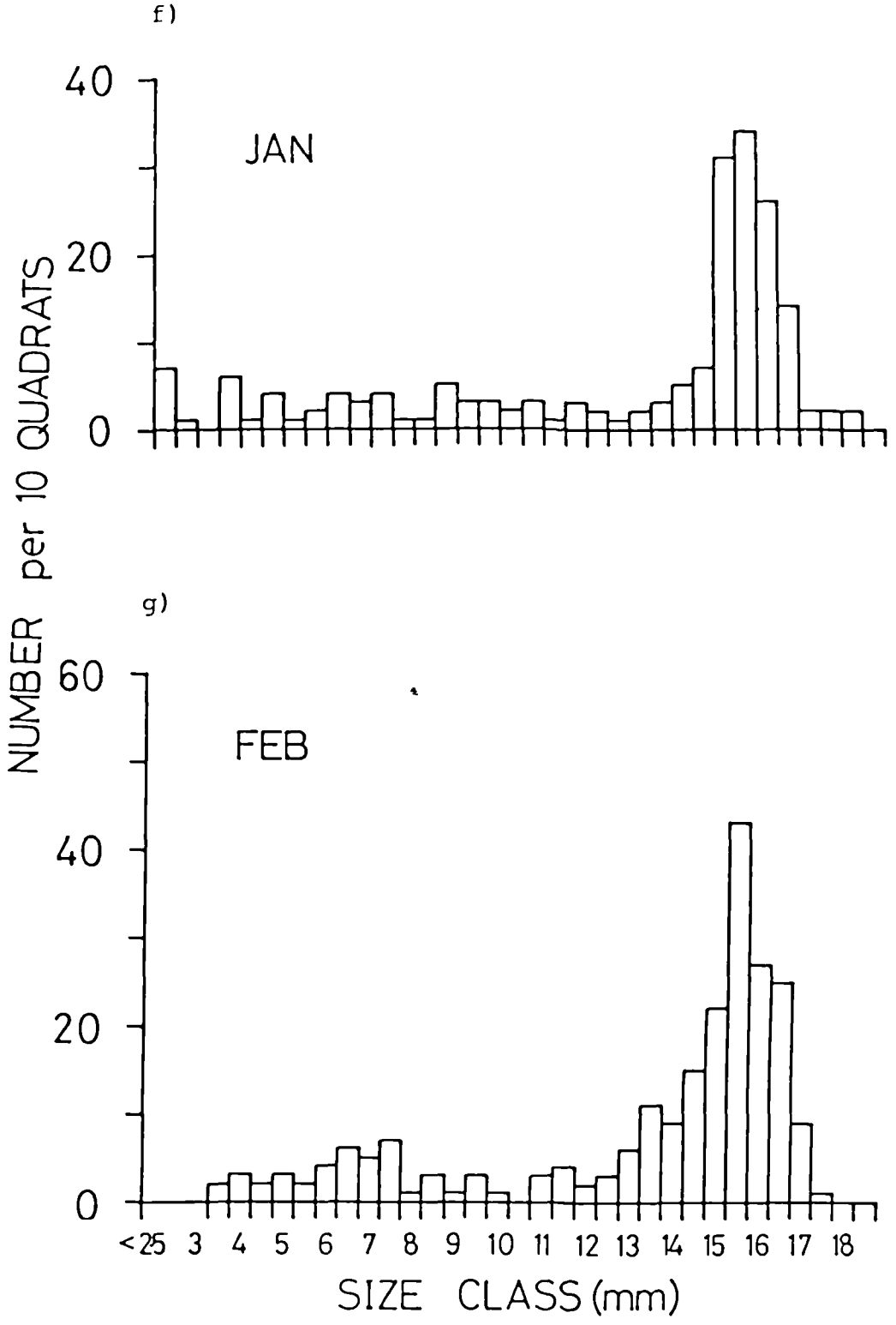
Figure 5.1
a) Size frequency histogram for L.obtusata from Sawdern in July 1986



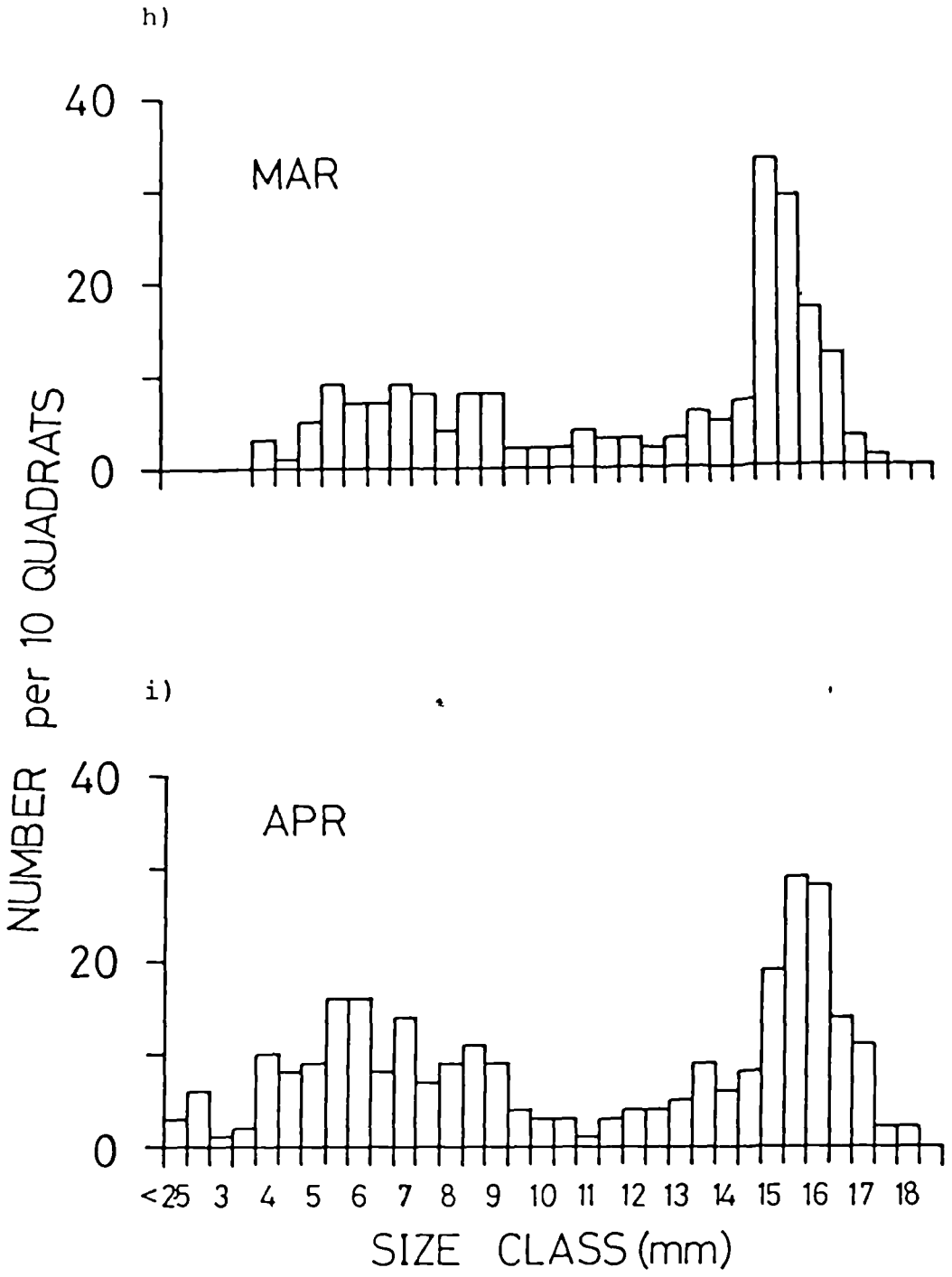
b and c) August and September 1986.



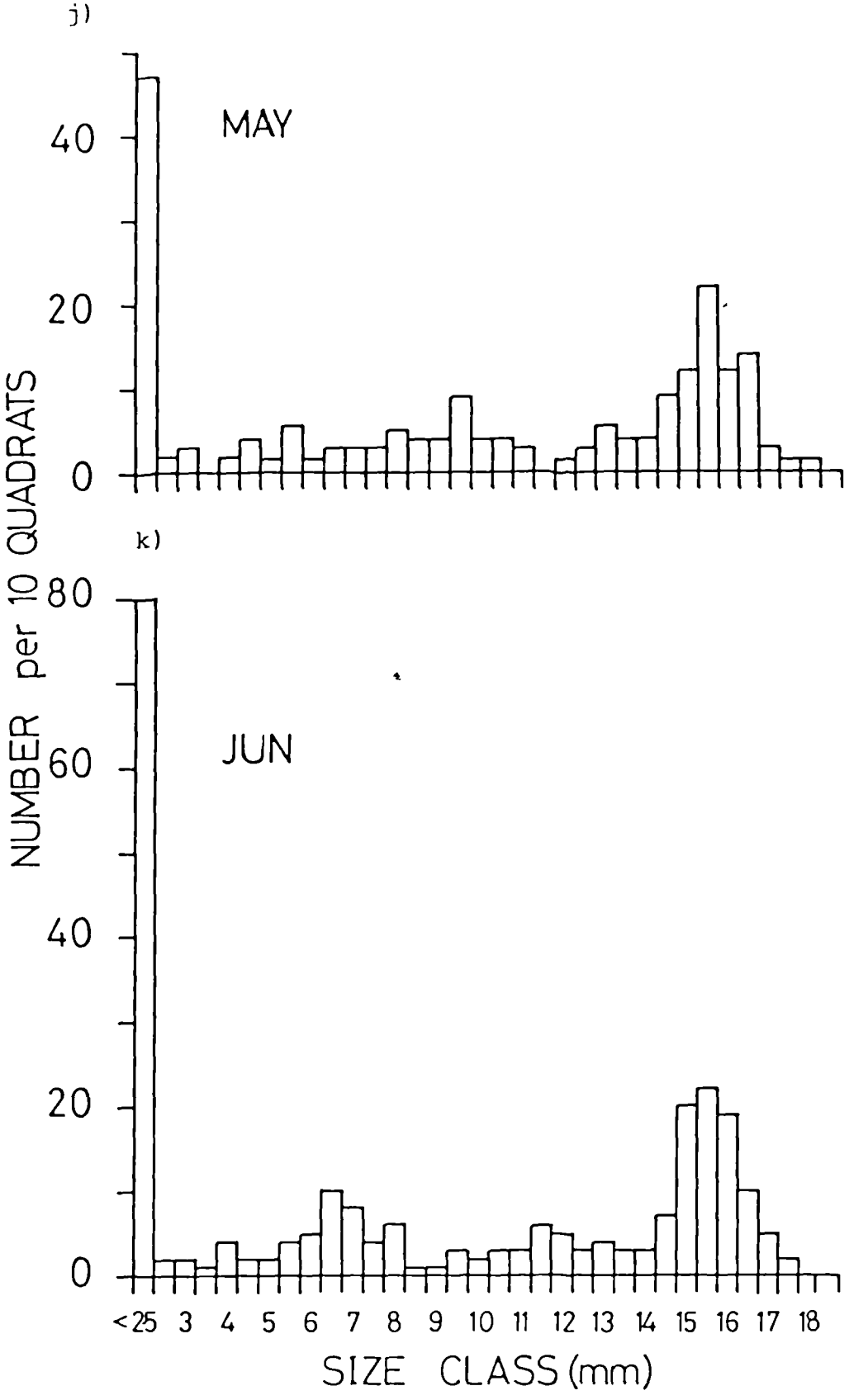
d and e) October and December 1986.



f and g) January and February 1987.



h and i) March and April 1987.



j and k) May and June 1987.

still scattered but became more structured in October. In October the numbers of newly hatched winkles had decreased and the juvenile component spread to include winkles up to 7-8mm. The adult peak was very similar to that of September and did not seem to have decreased in number. As previously mentioned the data for November are unavailable. In December the juvenile component was very small and appeared to merge with the other immature winkles. The adult peak was still present between 14-17mm. The further loss of the juvenile component of the population could be seen through January to March. In January there were a few newly hatched individuals but none were present in February or March. This lack of winkles below 4mm corresponded with the increasing build-up of a small peak of individuals in the size range 5-10mm. This was most clearly seen in February. During all these months the adult component was present and stable in the same size classes as previously described. In April there was an increase in the number of winkles below 3mm. During the next two months three main peaks of frequency could be seen. There was the increasing newly hatched component, which dominated the population in May, and a second distinct peak of immature winkles between 4-10mm. This peak is seen most clearly in April, where together with the adult component (between 12-18mm) it dominated the population structure. In May the total numbers of this immature component had dropped slightly. There was a slight shift along the graph in the frequency of individuals found, as the winkles approached adult size. For both these months the adult component was stable between 12-18mm.

The actual total numbers of L.obtusata decreased from approx 500 in July to around 200 in January-May. This loss was primarily comprised of juveniles but some adults were also lost in July and August. Newly hatched individuals continued to decrease in number until none were present in the late winter months. The adult component appeared to stabilise in September and the slight fluctuations after September can be attributed to juvenile loss and sampling irregularities. The total numbers appeared to increase after May as the young began to hatch. It was noticed during May that some of the fixed point quadrats had little algal cover (due to wave displacement) and that accounted for the drop in numbers. (A random quadrat at this level produced 3 times as many winkles as the sample.)

5.3.2 FUCOID COVER

Figure 5.2 shows the mean and S.D. values for the percentage cover of Fucoid algae recorded in 8 quadrats sampled in this investigation. (The 2 low shore quadrats were ignored as they only contributed 20% at the most of the L.obtusata population.) Throughout the period of the study the algal cover never dropped below 83% and was often closer to 95% cover. The variation around these values was slight, showing the cover to be stable and uniform in distribution.

5.3.3 L.mariae

Figure 5.3 (a to n) shows the size frequency histograms for L.mariae from April 1986 to May 1987. These

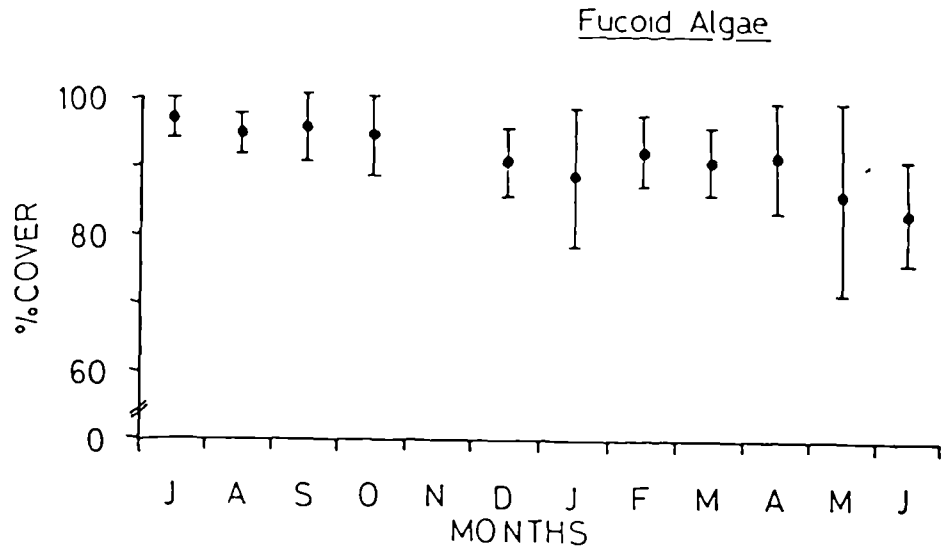


Figure 5.2
Mean and S.D. for fucoid cover at Sawdern from July 1986 to June 1987.

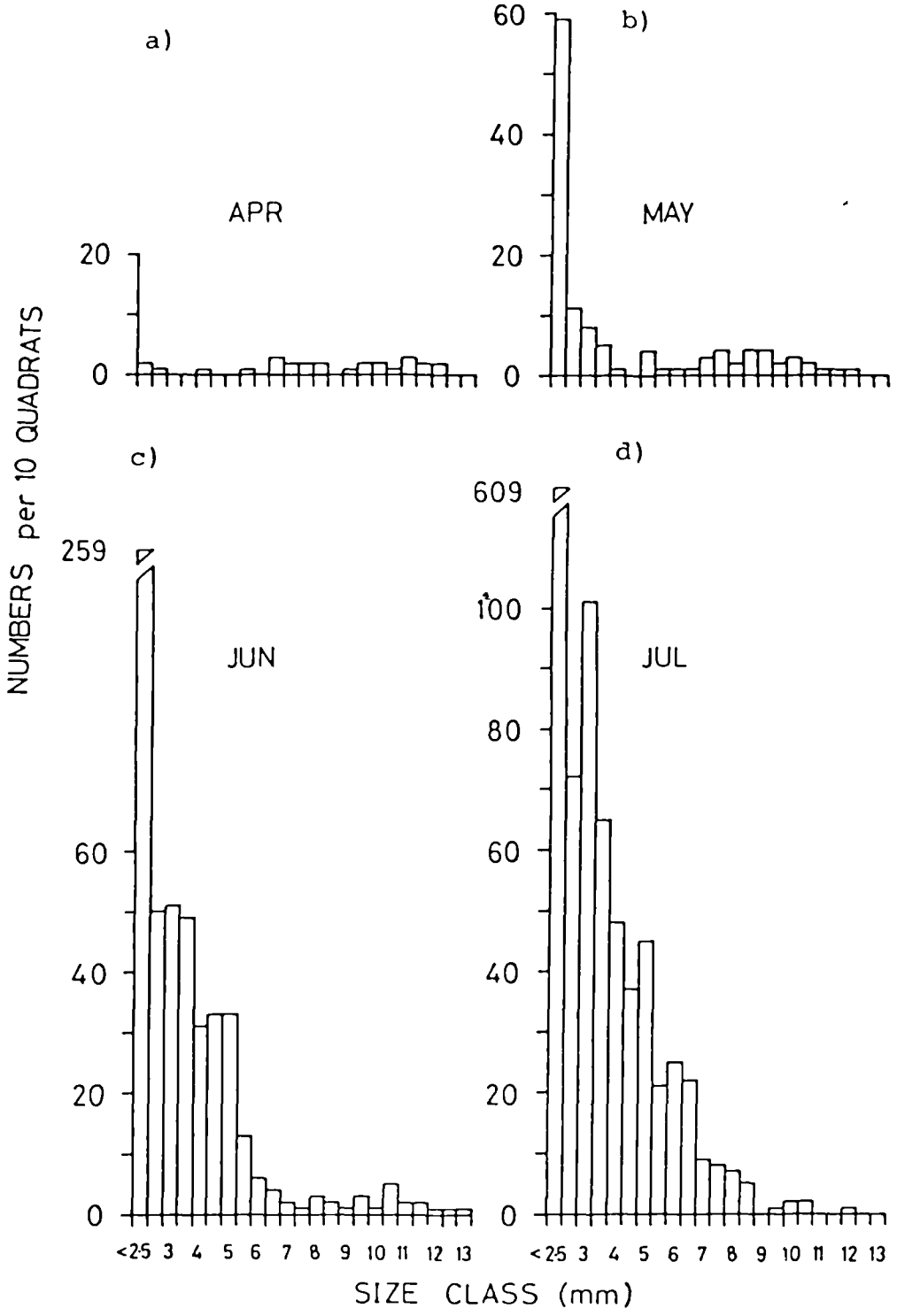
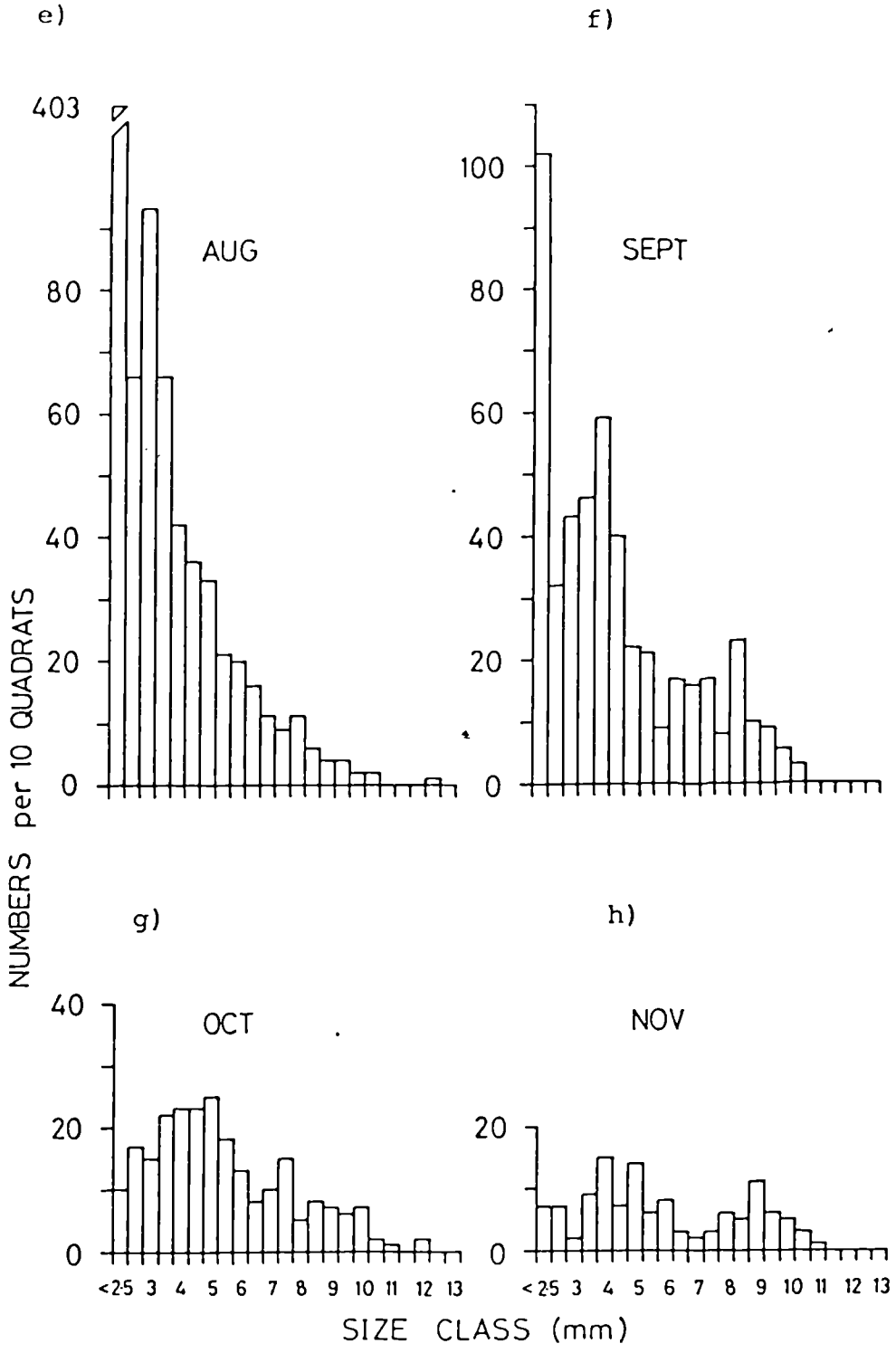
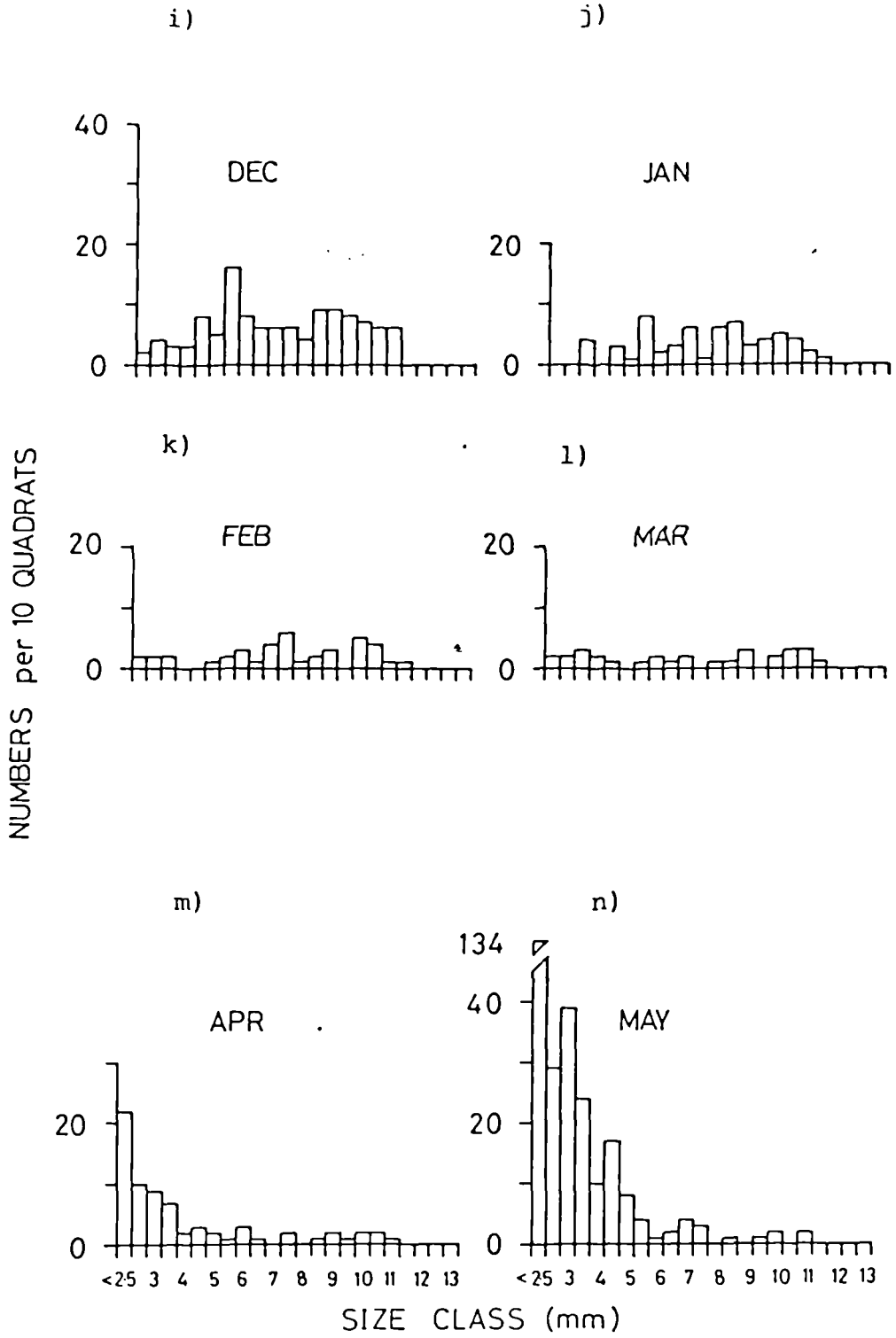


Figure 5.3
a to d) Size frequency histograms for L.mariae from Sawdern in April to July 1986.



e to h) August to November 1986.



i to n) December 1986 to May 1987.

results are very different to those for L.obtusata. In April 1986 there was a very sparse population of L.mariae present. This was made up of a number of different size classes. Individuals were scattered throughout these size classes, with a few juveniles in the low size classes; but mostly made up of individuals between 7-12mm. In May there was a large increase in juveniles, especially of those below 2.5mm. This peak was spread slightly ,with the juvenile component extending up to the 3mm size class. As in April, the rest of the population was low in frequency and distributed between the size classes 5-12mm. The juvenile component continued to increase and expand in June. The most numerous size class was, as in May, that below 2.5mm. This juvenile component of the population now formed the largest proportion of the population, spreading up to the 5mm size class. The remaining proportion of the population was made up of scattered individuals, up to the 13mm size class. In July the rapidly growing juvenile component continued to expand, reaching a peak of winkles below 2.5mm. This juvenile component extended as far as individuals of 8.5mm. The spread of this component continued into August when it reached the 10mm size class. The number of winkles below 2.5mm had begun to decrease and was lower than in July. In both these months the larger sized component of the population was becoming less frequent with only one or two individuals present.

In September there were no large individuals left and all the winkles found were contained in the size classes occupied by the growing juvenile component. This now ranged up to 11mm in size. The numbers of winkles

below 2.5mm continued to drop, as it did for all the other months after September until January when it began to pick up again. In October the spread of the juvenile component was still large and moving away from the smaller size classes. There was also a general decrease in total number of winkles in this month, and the differences between September and October represented a general difference in L.mariae's population. This pattern was followed in November, December and January with the major component of the population continuing to increase in size. In January there was no input from winkles below 2.5mm. In February there was a small input of these newly hatched winkles but the larger component of winkles continued to increase in size and were found in the 5-11mm size range. In this month the total numbers of winkles had drastically fallen and in March only scattered individuals were left along the entire size range. The increase in winkles below 2.5mm continued in April and the juvenile component of the population extended up to 6mm. There was a slight second peak in the size range 8.5-11mm, but there were very few individuals in this component. In May the juvenile component had vastly increased. The numbers below 4mm had dramatically risen and had spread along the size frequency axis. The number of individuals in the largest size classes had further decreased and only a few individuals were left in the size range 8.5-11mm.

The total numbers found increased from April 1986 to July 1986, most of this increase coming from very small winkles below 3mm. This was followed by a rapid decline in numbers during autumn and winter back to low values in

April 1987. This decline began in July and represents an almost negatively exponential survivorship line between July and November. In November the loss rate slowed slightly but the population plummeted again to reach levels as low as those for April 1986. In 1987 the lowest point reached was in March. After this a similar increase to that seen in 1986 was exhibited in April and May 1987, being due primarily to the influx of winkles below 2.5mm.

5.3.4 F.serratus COVER

Figure 5.4 shows the mean value and S.D. values for the percentage cover of F.serratus found in the 10 quadrats during this study. This shows how the amount of F.serratus increased from approx 70% in April to reach a maximum cover of 90% in June. It remained at this high level until it rapidly dropped in October. The cover continued to drop until in January it levelled out at approx 40% cover. From this trough the cover started to increase again, rising to reach a cover of 65% before sampling ceased. The distribution of F.serratus is very patchy as suggested by the large standard deviation values recorded, and was not as consistent as that of Ascophyllum at mid shore.

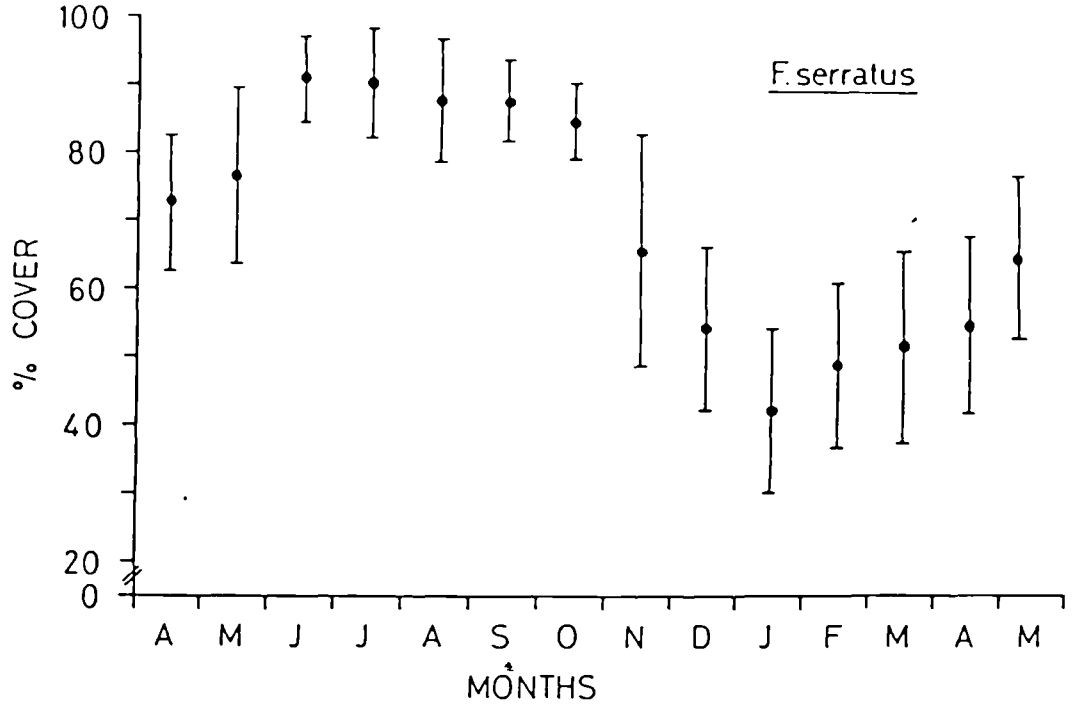


Figure 5.4
Mean and S.D. for F.serratus cover at Sawdern from April 1986 to May 1987

5.4 DISCUSSION

5.4.1 L.obtusata

The population dynamics of L.obtusata at Sawdern were similar to those reported by other workers at other sites (Goodwin 1975 at Aberystwyth; Hollingworth 1981 at the Menai Straits; Guiterman 1970 at Anglesey). The population structure was bimodal for most of the year and became trimodal briefly when the actively growing juvenile component was separated from the influx of newly hatched juveniles and the permanent adult population in April/May. For the rest of the year the population was composed of two groups - the stable adult population and the growing juvenile population. The peak of juvenile hatchings was seen in July and this component of the population gradually increased in size. The numbers of juveniles below 2.5mm decreased from July until February when there were no small individuals and this year's juvenile component was spread between the size range 5-10mm.

The adult component of the population was more stable. Adults remained in the 14-17mm size range. The adult numbers did fluctuate and were seen to decrease to a stable level after August. The higher numbers during the summer represent the recruitment of the previous year's juvenile component of the population. The subsequent decrease was probably the result of mortality of older winkles at the onset of winter. After this decrease the adult proportion of the population remained fairly constant over the winter. The slight fluctuations were probably artifacts of the sampling technique.

The two components of the population in this study were not as discrete as those recorded by Goodwin (1978). At Goodwin's site, despite egg hatching taking place throughout the summer and into early winter, the juvenile component remained discrete enough to allow the various components to be identified by polymodal growth analysis. Goodwin (1975, 1978) suggested that "some external factor is operating to prevent excess spreading of the juvenile group", and concluded that differential mortality related to timing of hatching may be important in maintaining this discrete component. As in this study, Guiterman's results (1970) were not as clear, and a complete differentiation between the components was rare. Such variation is not unexpected as the factors influencing the hatching and subsequent growth and development of the egg masses are themselves variable (for example macro- and micro- habitat differences, storms and extremes of the physical environment). Such events will affect growth and cause a merging of population components and a blurring of the overall structure. Despite this, it appears that the population dynamics of L.obtusata at Sawdern followed the scheme described by Goodwin.

The maintenance of such a structured and stable population, with a constant adult component that can live for 3-4 years, is reliant upon a temporally constant host alga. As shown by Figure 5.3 the amount of fucoid algae (principally Ascophyllum nodosum) never fell below 83% cover. Such a reliable algal resource would allow the maintenance of the complex life history shown by L.obtusata. The relationship between L.obtusata and

Ascophyllum is therefore extremely intimate. L.obtusata is attracted to both the complete alga and its exudates (Watson 1983). It is possible that the reliability of Ascophyllum as a resource has propagated this attraction of L.obtusata in an evolutionary sense. To continue a life style with little dispersal, as a result of laying benthic egg masses on the host alga, it is important that the host is both readily and constantly available. This is necessary for both short term growth of an individual and long term continuation of a population at any one place. The long lived (Baardseth 1970, Cousens 1981), perennial nature of Ascophyllum is therefore ideal for L.obtusata. The alga provides L.obtusata with a food source, a substrate to lay its eggs on and a refuge from predators (for adults via flo tation of the fronds and for juveniles by excavation of air-bladders).

Such specialization to exploit this resource has resulted in the avoidance by L.obtusata of potential competition with other gastropods for other algal resources (for example L.littorea for ephemeral greens; Watson and Norton 1985, Lubchenco 1978, Lacuna pallidula for F.serratus; Smith 1973, Grahame 1985, and many species for juvenile life-stages of other algal species). L.obtusata is the only species which is attracted to Ascophyllum and will feed on the alga (Watson and Norton 1985; 1987). This specialization provides L.obtusata with a unique and constant host alga. The long term stability of the alga is reflected in L.obtusata's long lived life history. L.obtusata is, however, not exclusively restricted to Ascophyllum as a host, and it is found on all fucoids (with

the possible exception of Pelvetia). This may suggest that all fucoids can be regarded as forming a potential niche for the species, but that it s optimum host and presumably most often realized niche is provided by Ascophyllum.

5.4.2 L.mariae

The results show that the population structure of L.mariae was very different from that of L.obtusata. In April there were very few individuals on the shore, most of which were between 7-12mm. In May there was a large recruitment of newly hatched juveniles. These extended from below 2.5mm to 4mm. The older individuals extended from 5-12mm. In June and July there was a rapid influx of juveniles, which were continually growing, extending the spread of this component to 7mm in June and 9mm in July. The previous year's adult component (i.e those above 7-9mm) decreased during these months, one or two individuals occupying the largest size classes. In August only one adult was found, all the other winkles being from the present year's juvenile component. These had now grown to reach the 10mm size class. The input of newly hatched individuals had decreased and more individuals were found in the larger size fractions. In September the decrease in winkles below 2.5mm continues and the juvenile component became more diverse showing two peaks, one at 4mm and one at 8mm. There were no longer any winkles in the largest size class (above 10.5mm). This trend continued into October, but the noticeable difference was the great decrease in the total numbers of winkles present. The numbers, especially of winkles below 5mm, dropped

dramatically and continued to drop until April of the next year. The population continued growing, with gradual recruitment into the larger size classes. The numbers of very small winkles also dropped until in January there were no winkles below 3mm left. In February some recently hatched winkles were present, and the other members of the population were scattered between the size ranges with a proponderance of individuals above 6mm. After this time the population increased as the newly hatched young were recruited into the population. In April and May of 1987 two components of the population were present: the newly hatched young and the survivors of the previous years recruits.

The population dynamics of L.mariae at Sawdern appeared to be similar to those of an annual species. Some adults did overwinter to reproduce and then the juveniles hatched out and grew rapidly to reach maturity by winter. As with many annuals there was a vast input of young which appear to suffer heavy mortality and failed to mature (Spight 1975). The adult breeding population was relatively small as compared to the influx of juveniles. The population dynamics of L.mariae closely resembled those of Lacuna pallidula. The life histories of these two species are very similar; both species live on and lay their eggs on F.serratus. The life history of L.pallidula has been studied in great detail (Smith 1973; Grahame 1977, 1982, 1985). It is a semelparous annual species and lives its entire life cycle on F.serratus. Its population numbers reach a peak in August to September after which they are subject to heavy mortality in the autumn.

Copulation takes place after the first die back and egg masses are laid in January to March. These develop after 2-3 months (their development is temperature-dependent) which accounts for the rapid increase in numbers in mid summer. This is very similar to the life cycle of L.mariae which also reached its highest population density in mid summer and suffered heavy mortality during the autumn/winter months. The survivors presumably breed and lay egg masses over the winter and early spring. As a result one or two old individuals will survive till the next peak of egg mass hatching.

The numbers which lived to breed, as compared to those that hatched, were small. These individuals can presumably produce vast numbers of eggs (c.f L.pallidula Grahame 1977), and the period of laying is greatly prolonged (Goodwin and Fish 1977). This, together with the slow development of egg masses laid in the winter months could account for the success of a small breeding population and the continuous wave of juvenile hatching in the spring and summer. In the case of L.pallidula this hatching time is synchronized with the production of new growth by F.serratus (Smith 1973). Smith showed that spawn was laid on young parts of the plant or new plants. The juveniles therefore hatched to a fresh, growing resource, which they could consume. At his sites Smith found a decrease in algal biomass due to lacunid grazing; this was not found in the present study as L.mariae is a micro-epiphytic browser. Smith's results for annual fluctuations in F.serratus were similar to those obtained in this study.

At Sawdern the increase in the numbers of L.mariae was closely synchronized with the increased growth of F.serratus. The onset of heavy mortality in the autumn was also correlated with the period of frond shedding and winter die-back of F.serratus. It seems logical that two species (L.mariae and L.pallidula) so totally dependent on F.serratus as a resource should show adaptations in their life-cycles to accommodate the temporal patchiness of this resource. The association of the die-back of L.pallidula and the winter die-back of F.serratus was not acknowledged by Grahame (1985). He suggested that predation by fish may be important. It is possible that size-dependent predation may play an important part in the mortality of L.mariae and L.pallidula, and this is discussed in Chapter 8.

Due to the non-destructive and time-intensive nature of the sampling method used in this study sex-ratios as obtained for L.pallidula (Smith 1973, and improved on by Grahame 1985) could not be calculated. This , together with detailed records of copulations and egg-mass laying and hatching would prove invaluable. The results from this study have not been replicated for other shores. It is possible that L.mariae only shows an annual life style on very sheltered shores. Further work should be attempted at more than one site to confirm the results obtained in this study.

Many authors have commented on the population dynamics of species relative to their body size. Natural selection will favour different life histories for species which have adults of different sizes (Spight et al. 1974). At low shore, natural selection favours the annual life

style: early maturity, rapid reproduction and short life-span. This is due to the unpredictability of adult survivorship, as a result of predation pressure (see Chapter 8) and resource depletion (frond shedding of F.serratus). It has been noted for other species that environmental instability results in selection for earlier sexual maturation and higher reproductive effort (Miller 1976, Spight and Emlen 1976). Such a strategy has the benefits of traditional "r" selected life styles: the species are opportunistic and can exploit temporally unstable resources. This is reflected in species body size (Calder 1984) and may explain the reduced size of L.mariae, when compared with L.obtusata.

L.mariae shows a style of life having rapid recruitment and reproduction combined with high mortality and a short life expectancy. This life style is dictated by natural selection imposed by living at low shore on F.serratus. Again this draws a close parallel with the lacunids L.vincta and L.pallidula which show a similar life style and which will be influenced by the same selective forces. L.obtusata lives at mid shore in Ascophyllum beds which provide a very reliable environment. Selection pressure will not be for L.obtusata to reproduce rapidly but rather to maximise its reproductive potential by being iteroparous and having a "K" style life history (see Spight and Emlen 1976, and Calder 1984). This is exactly the type of life style that L.obtusata possesses, having a slow development, a delayed reproduction and a relatively long life span.

6. GROWTH RATES

6.1 INTRODUCTION

The supposed effect of the competitive exclusion "principle" is to displace the niches of sympatric species so that they avoid competition between them for a limiting resource. This belief was first aired by Darwin (1888) who stated that "species in a state of nature are limited in their ranges by competition" and was supported by the experimental work of Gause (1934) which formalised the "principle." The principle is based on the over-use of a limiting resource by two or more species. This resource may take many forms, either biotic or abiotic; for example for food or space. Competition between species for food, i.e. between species on the same trophic level, is often the form of competition most readily visualised and investigated. Since L.obtusata and L.mariae represent two congeneric coexisting species it can be theorised, following the arguments of Den Boer (1986), that their niches, by definition, should differ significantly for one of two reasons: either

1) before meeting the species evolved separately and became adapted to the different parts of the shore, or

2) because they coevolved under pressure of competition they diverged in their resource utilization (Niche Shift).

The resolution of this theorising is virtually impossible, but it was hoped that the experiments undertaken in this chapter would provide useful information on the subject.

The major difference between L.obtusata and L.mariae

elucidated in Chapter 4 points to two possible niche dimensions which may have been limiting and are now distinct between the two species. These are the tidal height at which they live (and consequent time spent emersed-immersed) and their host weed species (L.obtusata living on Ascophyllum nodosum and L.mariae on Fucus serratus) Consequently their niche parameters associated with these differences vary accordingly. The results from the vertical transects also show that the species' vertical zonation patterns do overlap at the bottom of L.obtusata's tidal range and at the top of L.mariae's. This may represent a boundary between the partitioned potential niches of the two species. This section of work was devoted to studying the growth rates of the two species, both at their optimum tidal height and also when transplanted to the optimum tidal height of the other species. It was hoped that looking at growth responses would improve the picture which was imagined for the niche dimensions of the species. Combinations of the two species at the two tidal heights were also investigated, with the hope of observing possible interaction between the species.

Many workers have investigated the growth rates of L.obtusata and in many different ways. Guiterman (1970) examined L.obtusata populations in N.Wales and investigated growth rates using polymodal frequency analysis and also by enclosing animals in the laboratory and in nylon mesh bags from rafts and piers. Goodwin (1975) in West Wales also used polymodal frequency analysis and further improved the technique to discuss the breeding cycle and growth rates of L.obtusata (1978). Nylon mesh bags with pieces of weed

suspended in the water were also used by Wright (1976) to investigate growth in L.littoralis(sensu L.obtusata), and to compare the results with those for laboratory based animals. The most extensive study on L.obtusata growth rates was conducted by Hollingworth (1981) who used polymodal frequency analysis and mark-recapture methods via tags of paint and resin discs on cohorts of animals and individuals. He provided a detailed review of methods for growth estimation and their cost effectiveness. Other workers have looked at growth rates in L.obtusata/L.littoralis but their methods and species identification are poorly documented (Beland 1974, Daguzan 1976).

It seems that no workers have studied growth rates in L.mariae. All these experiments, except Hollingworth's, have involved extensive manipulation of the winkles' environment, if not grand scale destruction, or are laboratory based. Few have studied in situ growth. Therefore this section was devoted towards ascertaining growth rates of the two species at their respective tidal heights on the shore in as natural an environment as possible.

A very similar situation to the vertical zonation of L.obtusata and L.mariae has been described for Gibbula umbilicalis and Gibbula cineraria (Fretter and Graham 1962). It was suggested that the extension of the low shore G.cineraria upshore which is seen in the absence of G.umbilicalis is due to the loss of the superior competitor. However, as Underwood (1979) pointed out this is mere supposition; the factors that resulted in the

absence of G.umbilicalis could have proved beneficial to the extension of G.cineraria. This type of supposition requires manipulative field experiments to test these theories and it is to this end that the work in this Chapter is devoted.

Many workers have carried out such experiments on the rocky intertidal. This requires some form of containment or exclusion mechanism to maintain experimental conditions/populations. These usually take the form of cages, which although they alter the physical conditions of the shore are an indispensable tool for field ecology. Cages allow experiments to be done which could not be achieved by any other method (see Thayer 1985, Connell 1974). Using such cages various competitive relationships have been investigated either between predators and prey (starfish and mussels, Paine 1966) or between species competing for a limiting resource; for example barnacles competing for space (Connell 1961 b), limpets for food (Kitting 1980), limpets and snails for food (Underwood 1984 a&b) and winkle species competing for food (Behrens 1971,1974; Behrens Yamada and Mansour 1987) (for reviews see Underwood 1979, Connell 1974 and Hawkins and Hartnoll 1983). The present study has utilised the principles involved in these previous environmental approaches, but the details of the cages have necessarily been modified to suit conditions in dense algal beds.

6.2 MATERIALS AND METHODS

To investigate the aims previously set out the experiment needed to retain the experimental animals on the weed species found at their respective tidal heights and at the other species' tidal height. To investigate possible competition mixed species enclosures were also set up at each tidal height. This plan required some form of caging. The design of a suitable cage to contain winkles living on marine algae proved quite problematical especially for Ascophyllum as it often grows to over 3 metres in length at Sawdern and due to the air bladders floats when emersed.

Preliminary cage/enclosure designs were tested at Aust. The final design chosen consisted of a marine plywood base (approx 60cm x 60cm = 3600cm sq) with wire mesh caging attached and is shown in Plate 6.1. The wire was coated in black plastic (resulting in a mesh diameter of approx 4.5mm) and bolted onto the plywood with brass bolts to form a square (approx 50cm x 50cm =2500cm sq). The caging was moulded in such a way as to provide easy attachment of the plastic mesh and to have a lip that the winkles would have difficulty climbing. The caging was constructed in "L" shapes so that each plywood base had two joined pieces per cage. At each corner of the wire foam rubber was used as a seal between the cage and plywood (Lein 1984). All the other seals were checked and considered sound. To aid drainage the plywood was drilled with small holes. To each of these cages was sewn black plastic netting ("Netlon" diameter 5mm). These were sewn

Plate 6.1
Design of cages used in the experiment. The smaller cage was used to contain F.serratus at low shore; and the larger cage for A.nodosum at mid shore.

to heights of either 100cm, to enclose Ascophyllum, or 50cm to enclose F.serratus.

The tidal height used dictated the weed in the cage: mid shore cages containing Ascophyllum and low shore cages F.serratus. The amount of algae placed in each cage was based on the seaweed cover of five 50cm x 50cm quadrats of each weed at their respective heights. This alga was wet-weighed (using a spring balance) and the mean value taken. The value obtained was halved and taken to represent half the quadrat's cover. This sample alga was then spread over a plastic sheet and used as a standard. Alga was collected attached to lumps of rock and selected so that its size appeared equal to that of the standard algae. This purely subjective method was used because it was impossible to weigh algal samples attached to rock. As the algae represented half a quadrat's cover, the winkle densities were chosen accordingly using the data from vertical height transects (see Chapter 4 and Population Dynamics, Chapter 5). In the case of L.obtusata the mean value per quadrat at the height chosen was stable throughout the year at 60 winkles, so the optimum cage density was chosen as 30 winkles per cage. For L.mariae the decision was more difficult due to the large seasonal variation shown by the population as a result of the annual life cycle shown by the species at Sawdern (see Chapter 5). Therefore the number chosen was a compromise between the number expected at the time of year at which the experiment would end (approx 20 per quadrat) and the large numbers of small winkles found at the time the experiment was set up. It was decided that 30 L.mariae would be used per cage

which would provide a simple comparison with L.obtusata.

Winkles were collected at their respective tidal heights on the shore. It was decided to enclose the smallest winkle size possible for the mesh size used in order to achieve maximal growth potential for the duration of the experiment. The winkles collected were measured, using vernier calipers, to the nearest 0.05mm. They were then engraved using a mini drill with a dental burr bit, marking with a single stripe on the top of the shell. The purpose of this mark was to differentiate the experimental animals from non-experimental animals which may have crawled into the cages. Unfortunately time did not allow engraving of individual numbers on the winkles. Previous trials with paint marking had proved unsuccessful and the necessary drying time possibly harmful to the snail due to desiccation. The snails were then weighed having been blotted with tissue paper. The balance used was a portable Ni-Cd battery operated model accurate to 0.02g (A&D Electronic Balances Model EW-60 B).

The snails were then placed in the prepared cages. Each cage had a piece of the sample algae attached to a rock which had been cleared of winkles by hand and placed in the centre of the cage. The bottom of the cage was then filled with rocks, all of which were checked for the presence of other macro-algal grazers or other species which could potentially affect the experimental winkles. The winkles were then shaken onto the weed surface and the cages sewn up. The protruding plywood bases were then weighted down with boulders so the cages were immovable on the shore.

The experimental design allowed for 12 cages at each tidal height, each cage containing algae from that respective height. These cages were used for 4 replicates of 3 treatments. The first treatment was the species of winkle normally found at that tidal height; the second was of the other species, and the third was of a mixture of the two species. It was hoped to increase the densities of the winkles in this third treatment but time proved limiting. The exact design is shown in Table 6.1.

Table 6.1
Experimental design for the growth rate experiment.

MID SHORE-algal species = Ascophyllum nodosum

30 L.obtusata	30 L.mariae	30 L.obtusata/30 L.mariae
30	30	30/30
30	30	30/30
30	30	30/30

No cages 4 4 4 =12
No winkles per cage=30/ species

LOW SHORE-algal species = F.serratus

30 L.obtusata	30 L.mariae	30 L.obtusata/30 L.mariae
30	30	30/30
30	30	30/30
30	30	30/30

No cages 4 4 4 =12

TOTAL Number of cages =24

6.3 RESULTS

The results from this experiment can be divided into four sections:

(1) Cage design and recapture rates.

(2) Increases in shell size and weight.

(3) Effects of grazing on host algae.

(4) Relative growth rates.

6.3.1 CAGE DESIGN AND RECAPTURE RATES

The cage design proved quite effective. The major problem was storm damage after gale force winds in August. This primarily affected the mid shore cages which, due to their height, tended to bend and rip under the strong winds and the weight of surrounding Ascophyllum. As a result nearly all the mid shore cages were damaged, a few very badly. These were repaired as soon as possible by "sewing" the caging with electrical cable tags. The low shore cages suffered less damage, their smaller size giving the cages more rigidity. Of these only three were damaged; none badly.

Recaptures of experimental animals from the mid shore cages were therefore lower than was hoped due to the rips in the netting and subsequent escapes of the snails. Table 6.2 shows the number of winkles recaptured and found dead in the cages. The overall recapture rate was 37% over 117 days as compared to 63% over the first 56 days. For the low shore cages the recapture rate was very high, being above 80% after both 56 days and 117 days.

The losses from the cages could represent escapes, predation or mortality and subsequent shell abrasion.

Table 6.2
Recapture and mortality rates for the experimental animals after 56 and 117 days.

	MID SHORE				LOW SHORE			
	L.ob S	L.ob M	L.ma M	L.ma S	L.ob S	L.ob M	L.ma M	L.ma S
After 56 days								
No Alive	78	103	41	25	113	112	91	104
No dead	0	0	6	12	1	0	0	2
Recapture	65%	86%	39%	31%	95%	93%	76%	87%
After 117 days								
No Alive	56	65	7	12	110	100	91	93
No dead	0	1	16	15	1	4	3	7
Recapture	47%	55%	20%	23%	93%	87%	78%	83%

KEY
L.ob = L.obtusata
L.ma = L.mariae
S = single species cages
M = mixed species cages

Shell fragments and dead shells were found in many cages. The recapture rates include dead shells as recaught individuals. The data show that the mid shore sites lost the most winkles. It appears, however, that L.mariae was lost to a greater extent than L.obtusata, and this was also true of the low shore site: for both the single-species enclosures and the mixed-species cages L.mariae was lost at a faster rate than L.obtusata. This may represent L.mariae escaping more readily than L.obtusata, or L.mariae dying and their shells being washed out of the cages or abraded into debris. Dead shells found in the cages were positive indications of winkle mortality. More dead L.mariae shells were found than L.obtusata and this was most pronounced for the mid shore site. To test whether significantly greater numbers of L.mariae died at mid shore than any of the other treatments a Chi-Square test was applied. This showed that there was a significantly greater (Chi-square of 37.1, for 1 degree of freedom, $P<0.001$) mortality for L.mariae at mid shore than any of the other treatments.

6.3.2 INCREASE IN SHELL SIZE AND WEIGHT

Tables 6.3-6.4 show the results for the growth of the winkles in the enclosure experiments giving the means and standard deviations for the increase in shell size (in mm) and weight (in g) for all the treatments.

The mean values for the increase in size and weight of the winkles in their respective treatments are plotted in Figures 6.1 for increase in shell size and Figure 6.2 for increase in shell weight. The increase in size of L.obtusata varied greatly between the mid shore and low shore sites; but very little between the single-species and

Table 6.3
Mean and standard deviations for shell size of winkles after 56 and 117 days.

MID SHORE	INITIAL SIZE	AFTER 56 DAYS	AFTER 117 DAYS
L.obtusata (S)	8.03±0.09	9.57±0.20	10.85±0.10
L.mariae (S)	7.80±0.07	8.64±0.15	9.13±0.45
L.obtusata (M)	7.91±0.13	9.58±0.13	10.94±0.12
L.mariae (M)	7.80±0.20	8.74±0.18	8.96±0.51
LOW SHORE			
L.obtusata (S)	8.13±0.11	10.56±0.19	12.08±0.26
L.mariae (S)	7.88±0.02	9.21±0.29	9.65±0.15
L.obtusata (M)	8.09±0.11	10.69±0.10	12.14±0.06
L.mariae (M)	7.80±0.13	9.06±0.22	9.53±0.18

KEY
(S) = single species cages
(M) = mixed species cages
The mean values represent the values for all four replicates.

Table 6.4
Mean and standard deviations for shell weight (g) of winkles after 56 and 117 days.

MID SHORE	INITIAL SIZE	AFTER 56 DAYS	AFTER 117 DAYS
L.obtusata (S)	0.25±0.008	0.40±0.022	0.60±0.018
L.mariae (S)	0.24±0.01	0.30±0.021	0.03±0.047
L.obtusata (M)	0.24±0.009	0.41±0.012	0.62±0.015
L.mariae (M)	0.24±0.01	0.30±0.021	0.03±0.040
LOW SHORE			
L.obtusata (S)	0.26±0.013	0.54±0.026	0.82±0.046
L.mariae (S)	0.24±.0005	0.36±0.036	0.43±0.032
L.obtusata (M)	0.25±0.015	0.58±0.015	0.83±0.012
L.mariae (M)	0.24±0.019	0.35±0.017	0.40±0.026

KEY
(S) = single species cages
(M) = mixed species cages
The mean values represent the values for all four replicates.

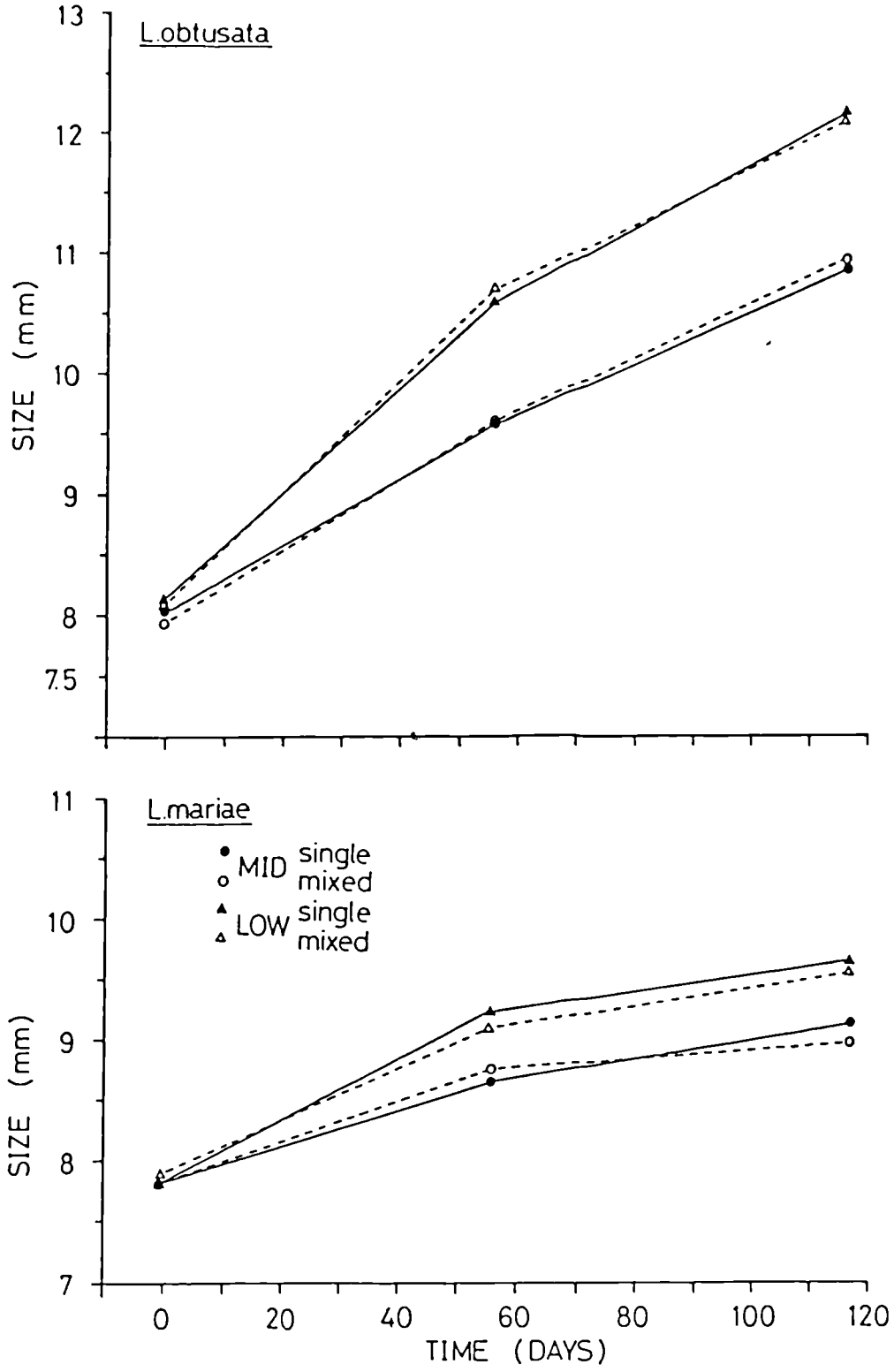


Figure 6.1
Increase in shell size for L.obtusata and L.mariae at Sawdern after 56 and 117 days respectively (for S.D. values consult Table 6.3).

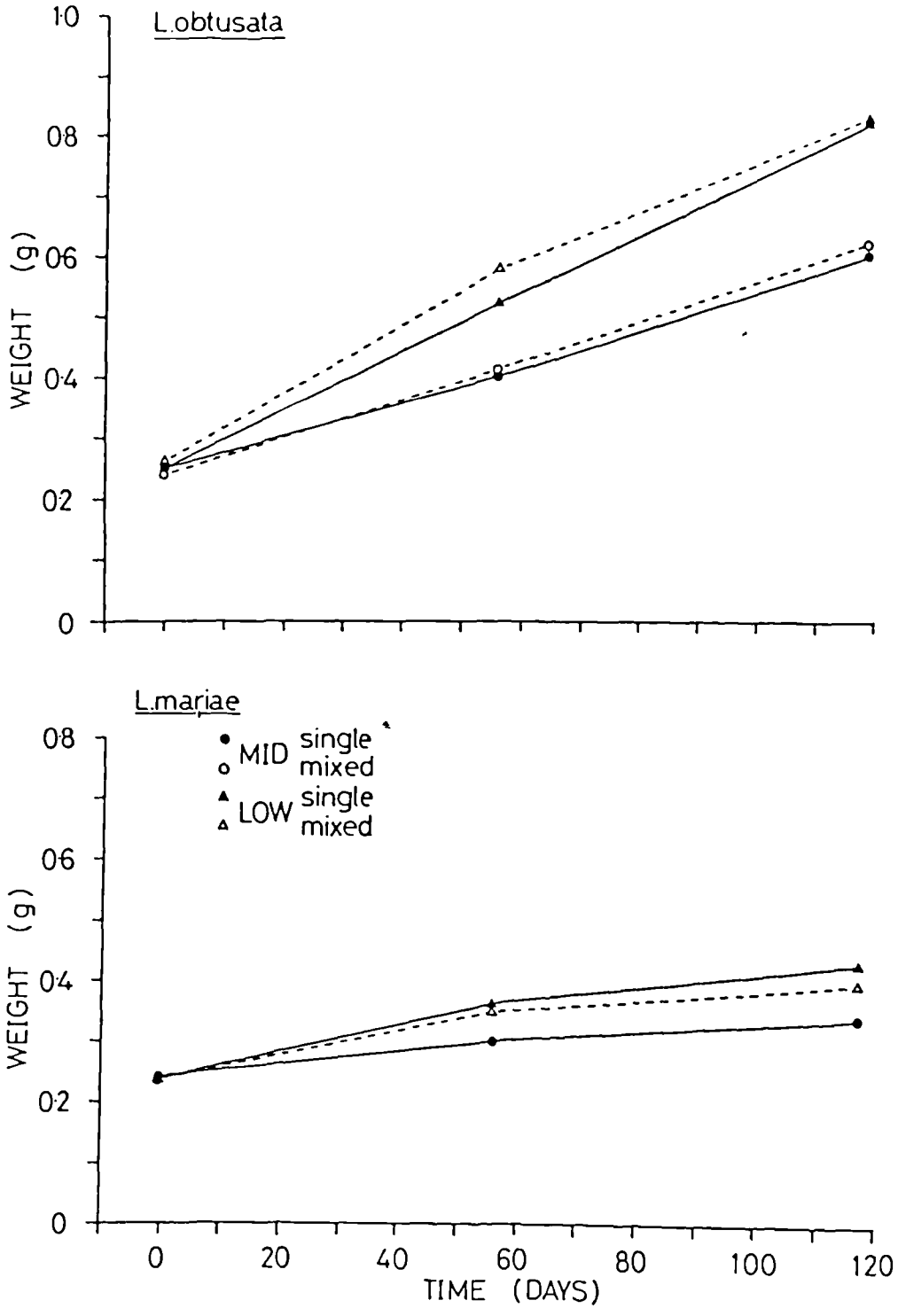


Figure 6.2
Increase in weight of L.obtusata and L.mariae at Sawdern after 56 and 117 days respectively (for S.D. values consult Table 6.4).

mixed-species stands. The graphs show that shell size in L.obtusata increased more at low shore than at mid shore. L.obtusata was larger at the low shore sites after both 56 days and 117 days. There was hardly any difference between the treatments of single-species and mixed-species stands, the lines mimicking each other.

The increase in shell size of L.mariae differed slightly from that of L.obtusata. L.mariae grew to a larger size at low shore than at mid shore after both 56 and 117 days, but the difference was not as pronounced as that for L.obtusata. The close relationship between the mixed-species and single-species treatments seen for L.obtusata was also seen for L.mariae. At low shore L.mariae grew slightly larger in cages by itself than it did in mixed stands with L.obtusata. This was also the case for the small number of L.mariae left at mid shore after 117 days, the difference being reversed after 56 days. These differences were all slight.

The increase in weight for the two species showed a similar pattern. L.obtusata at low shore sites increased in weight faster than those at the mid shore sites. L.obtusata in the mixed-species cages at low shore after 56 days appeared to have increased in weight more quickly than those in single-species stands, but after 117 days there was little difference between the two treatments. This pattern is therefore similar to that for shell-size increase in L.obtusata. The same pattern was also maintained for L.mariae. As in shell size the low shore caged animals increased in weight faster than the mid shore animals. There was virtually no difference between the

mixed or single-species stands at mid shore, the mean values being identical. At low shore, however, the single species stand of L.mariae seemed to do slightly better than in a mixed stand in the presence of L.obtusata.

6.3.3 EFFECTS OF GRAZING ON HOST ALGAE

There was a large difference in the quality of the algae remaining in the low shore cages at the end of the experiment. In the L.mariae single species cages the F.serratus was perfectly healthy and resembled uncaged algae at this shore level. The F.serratus in cages which contained L.obtusata was very ragged and depleted. The winkles had gouged large chunks and holes from the alga. This is shown in Plate 6.2 and illustrates the different modes of feeding of the two species, L.mariae being principally a micro-algal grazer browsing epiphytes off the surface of the algae, and L.obtusata being a macro-algal grazer excavating the thallus of the alga.

6.3.4 RELATIVE GROWTH RATES

In order to obtain a more accurate assessment of the relative increases in weight and shell size of the two species under the different treatment regimes, relative growth rates were calculated using the following formula:

$$r = \frac{\log_e (\text{mean } t \,/\, \text{mean } 0)}{t}$$

(Underwood 1979 b)

Where t = is time in days of sample

0 = initial time of sample

r = relative growth rate

Table 6.5 shows the growth rates for shell size.

Plate 6.2
Effect of grazing on F.serratus. The alga on the top left has been in a L.mariae cage and the alga on the top right in a L.obtusata cage. The bottom picture shows a detail of L.obtusata feeding on a F.serratus frond.

Table 6.5
Mean and standard deviations for shell growth rates (mm/day x 10-3) of winkles after 56 and 117 days.

	AFTER 56 DAYS	AFTER 117 DAYS
MID SHORE		
L.obtusata (S)	3.13±0.44	2.07±0.32
L.mariae (S)	1.84±0.47	0.76±0.607
L.obtusata (M)	3.42±0.104	2.17±0.0081
L.mariae (M)	2.02±0.31	0.47±0.429
LOW SHORE		
L.obtusata (S)	4.64±0.443	2.22±0.21
L.mariae (S)	2.77±0.38	0.77±0.365
L.obtusata (M)	4.97±0.143	2.01±0.173
L.mariae (M)	2.67±0.37	0.83±0.364

KEY
(S) = single species cages
(M) = mixed species cages
The mean values represent the values for all four replicates.

These are presented graphically in Figure 6.3. The growth rates for shell size show similar trends to those described for gross increase in shell size. This is also true for the weight growth rates which are shown in Table 6.6 and illustrated in Figure 6.4. These trends were tested for significance using Analyses of Variance. No live L.mariae individuals were recaptured from two of the mid shore cages. In order to balance the subsequent analysis, values were calculated which did not affect the mean or standard deviation of the treatments' remaining replicates (Snedecor and Cochran 1967). To investigate which of the factors of the experiment were important to the growth of the winkles a 4 factor ANOVA was conducted to compare the factors Height (mid and low shore); Species (L.obtusata and L.mariae); Time (56 and 61 days) and Mixed/Alone (single species and mixed species stands). The analysis in Table 6.7 shows that the factors height, species and time were significant. Therefore subsequent analysis concentrated on these 3 factors combining mixed and single species stands to give the cell means used in further analysis 8 replicates. The shell size and weight growth rates were compared by 3 way ANOVA and the results are presented in Tables 6.8 and 6.9. Significant differences were further analyzed using SNK Tests as shown at the bottom of the ANOVA Tables.

The results from these analyses confirm the trends described. For both variables, shell size and weight, the three main factors were all significant as were the interactions between time and height (winkles grew faster after 56 days at low shore and 61 days at mid shore than

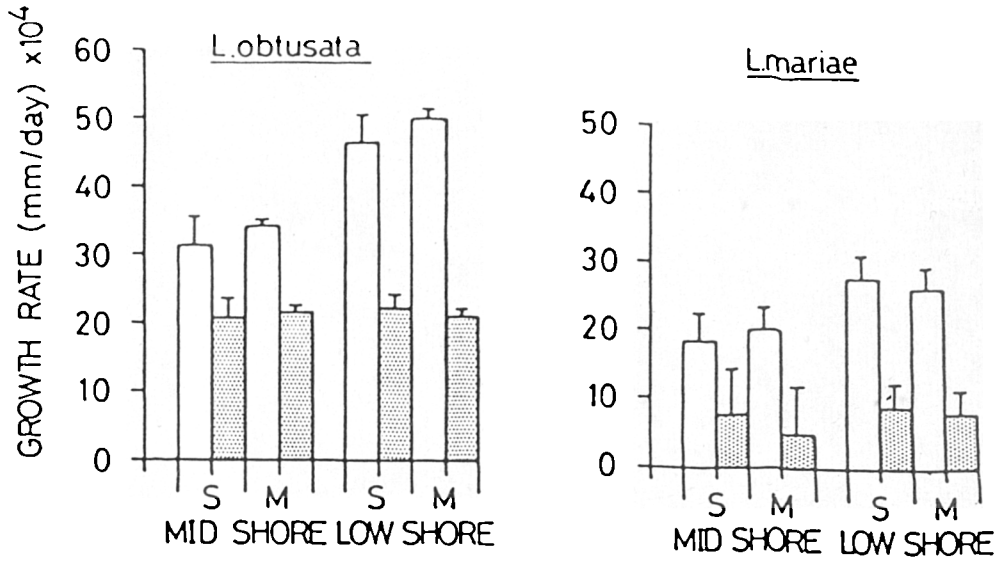
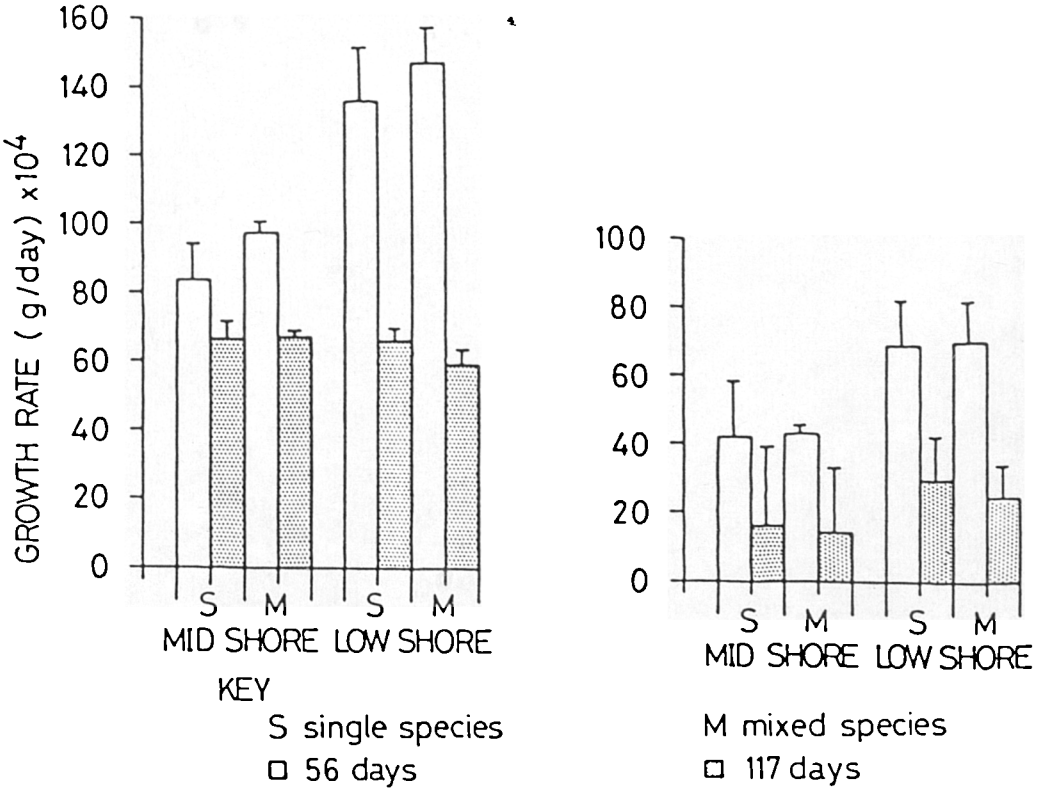


Figure 6.3
Mean relative growth rates for shell size, and S.D. bars for L.obtusata and L.mariae after 56 days (clear) and 117 days (stippled) at Sawdern.



Figue 6.4
Mean relative growth rates for weight, and S.D. bars for L.obtusata and L.mariae after 56 days (clear) and 117 days (stippled) from Sawdern.

Table 6.6
Mean and standard deviations for shell weight growth rates (g/day x 10-3) of winkles after 56 and 117 days.

MID SHORE	AFTER 56 DAYS	AFTER 117 DAYS
L.obtusata (S)	8.38±1.00	6.66±0.44
L.mariae (S)	4.19±1.71	1.44±1.94
L.obtusata (M)	9.75±0.33	6.68±0.14
L.mariae (M)	4.36±0.54	1.39±1.14
LOW SHORE		
L.obtusata (S)	13.48±1.54	6.66±0.41
L.mariae (S)	6.99±1.37	2.94±1.38
L.obtusata (M)	14.78±1.05	5.95±0.44
L.mariae (M)	7.13±0.93	2.39±1.05

KEY
(S) = single species cages
(M) = mixed species cages
The mean values represent the values for all four replicates.

Table 6.7
Three Way Analysis of Variance to investigate the relative importance of the factors analyzed during the experiment.

SOURCE OF VARIATION	DF	MEAN SQ	F	SIGNIFICANCE
TIME	1	1239	83	* * *
HEIGHT	1	160	10.8	*
SPECIES	1	990	66	* * *
MIXED/ALONE	1	1.2	0.08	N.S
RESIDUAL	11	14.36		
TOTAL	15			

KEY
* = $P < 0.05$; * * * = $P < 0.001$; N.S = Not significant

FACTORS
TIME = 56 days v's 61 days
HEIGHT = mid shore v's low shore
SPECIES = L.obtusata v's L.mariae
MIXED/ALONE = single species v's mixed species cages

Therefore important factors are TIME, HEIGHT and SPECIES

Table 6.8
Three Way Analysis of Variance to investigate the variation in shell growth rate during the experiment. The significant results of a SNK Test are shown at the bottom of the ANOVA table.

SOURCE OF VARIATION	DF	MEAN SQ	F	SIGNIFICANCE
TIME	1	4958	389	* *
HEIGHT	1	643	50	* *
SPECIES	1	3964	311	* *
TIME X HEIGHT	1	443	35	* *
HEIGHT X SPECIES	1	35	2.7	N.S.
TIME X SPECIES	1	34	2.6	N.S.
TIME X HEIGHT X SPECIES	1	79	6.2	*
RESIDUAL		53	12.76	
TOTAL		60		

KEY
* = P < 0.05; * * = P < 0.01; N.S. = Not significant

FACTORS
TIME = 56 days v's 61 days
HEIGHT = mid shore v's low shore
SPECIES = L.obtusata v's L.mariae

SNK Test

L.ma = L.ma < L.ma = L.ob = L.ob < L.ma < L.ob < L.ob
61 Mid 61 Low 56 Mid 61 Mid 61 Low 56 Low 56 Mid 56 Low

Table 6.9
Three Way Analysis of Variance to investigate the variation in shell weight growth rate during the experiment. The significant results of SNK Test are shown at the bottom of the ANOVA table.

SOURCE OF VARIATION	DF	MEAN SQ	F	SIGNIFICANCE
TIME	1	30455	243	* *
HEIGHT	1	7593	61	* *
SPECIES	1	43144	344	* *
TIME X HEIGHT	1	4881	39	* *
HEIGHT X SPECIES	1	41.7	0.33	N.S.
TIME X SPECIES	1	872	6.95	*
TIME X HEIGHT X SPECIES	1	1528	12.2	* *
RESIDUAL	53	125.47		
TOTAL	60			

KEY
* = P < 0.05; * * = P < 0.01; N.S. = Not significant

FACTORS
TIME = 56 days v's 61 days
HEIGHT = mid shore v's low shore
SPECIES = L.obtusata v's L.mariae

SNK Test

L.ma = L.ma = L.ma < L.ob = L.ob = L.ma < L.ob < L.ob
61 Mid 61 Low 56 Mid 61 Mid 61 Low 56 Low 56 Mid 56 Low

after 56 days at mid shore and 61 days at low shore) and the three way interaction. The interaction between height and species (L.obtusata after 61 days and L.mariae after 56 days gaining weight faster than L.obtusata after 56 days and L.mariae after 61 days) was also significant for the increase in weight of the winkles.

The results of the SNK Tests show the effects of the experiment most clearly. From measurements of shell size, L.mariae in the second 61 days at both mid and low shore grew at a similar rate to L.mariae at mid shore in the first 56 days. L.obtusata, at both mid and low shore, in the second 61 days grew at a similar rate to L.mariae in the first 56 days at low shore, growing significantly faster than the treatments of L.mariae previously described. The remaining L.obtusata treatments grew at a significantly still faster rate, so that L.obtusata at low shore in the first 56 days grew faster than L.obtusata at mid shore in the same time period.

The increase in weight showed that the L.mariae treatments after 61 days at both low shore and mid shore, and after 56 days at mid shore, had similar growth rates. These were significantly slower than L.obtusata at mid and low shore after the second 61 days, and L.mariae after 56 days at low shore, all of which had similar growth rates. As for the growth rates based on shell size, L.obtusata at mid shore after 56 days grew significantily faster than the other treatments, except for L.obtusata after the same time period at low shore, which had the fastest growth rate.

In conclusion both species grew significantly faster in the initial 56 days than the next 61 days. L.obtusata

grew faster than L.mariae. L.obtusata also grew faster when transplanted to low shore than it did at mid shore where it is normally found. The reverse was true for L.mariae which grew faster at low shore, in its normal home range, than when transplanted to mid shore. L.obtusata grew faster for the first 56 day period than the next 61 days, its rate of shell size increase decreasing during the second time period. Snails in the low shore treatments both grew faster than the mid shore treatments in the initial 56 days period. Between 56 and 117 days, however, the mid shore and low shore cages grew at a very similar rate for all the treatments. There was a slight difference in the rates between treatments at the same tidal height. Up to 56 days the mixed treatments grew faster than the single populations but from 56 days to 117 days this effect was less pronounced. Overall, the mixed populations increased in shell size faster than did the single species stands.

6.4 DISCUSSION

6.4.1 CAGE DESIGN AND RECAPTURE

The discrepancy between the numbers of the two species retained in the cages, especially at mid shore, indicates a possible difference in the "loss" rates of the winkles. These losses can be attributed to predation, escape or mortality. At mid shore L.mariae had a higher rate of loss due to one, two or all these factors. Differential predation is unlikely as a factor, because at these sizes L.mariae is better protected against crab attack than L.obtusata due to its increased thickening (Reimchen 1984). Although the cages were damaged, allowing access by crabs, they would still have prevented access by fish and birds. Crabs are therefore the only form of predator that could affect the winkles.

It is possible that L.mariae is more likely to escape than L.obtusata. Personal observations showed L.mariae to be far more active than L.obtusata at low water. L.mariae appeared on the surface of the weed actively browsing and even crawling over the interior of the cage, while L.obtusata retreated into the centre of the weed clump. It therefore follows that L.mariae's increased behavioural activity would have resulted in the species being more likely to encounter rips in the cage and therefore escape via these routes. The more sedentary nature of L.obtusata resulted in this species being retained even in the very badly damaged cages.

The third solution is that L.mariae suffered increased mortality as compared to L.obtusata, and due to

abrasion some of the dead shells were broken down in the bottom of the cage. A number of dead L.mariae shells were found in many cages, the largest number being at mid shore. This figure was far greater than for L.obtusata. The greater loss of L.mariae from the mid shore cages can therefore probably be attributed to a combination of increased activity and therefore escape, and increased mortality at this height. A chi-square test showed that significantly more L.mariae were found dead at mid shore as compared to low shore.

The high recapture rate of both species at low shore is an indication of the success of the cages at retaining the winkles if they remained undamaged. It also demonstrated that the cages did not, by themselves, cause high mortality.

6.4.2 GROWTH RATES AND INTERACTION WITH HOST ALGAE

The growth results show both intra- and inter-specific differences. Comparison of the growth of the two winkle species is not straightforward. It should be remembered that the mean adult sizes of L.obtusata at Sawdern were 16.3mm for females and 16.1mm for males and that after 117 days the experimental animals were approaching 10-12mm. Therefore they still had a great growth potential to realise. Conversely the mean adult size of adult L.mariae at Sawdern was 10.1mm for females and 8.3mm for males and the experimental animals were almost realising this maximal size as they ranged from 8.5-9.5mm. Therefore their growth rates and size/weight increases would have been comparably less than those for L.obtusata.

The most "natural" treatments were with the species placed at their correct tidal heights; L.obtusata growing at mid shore on Ascophyllum, and L.mariae at low shore on F.serratus. For L.obtusata in the summer months (i.e the first 56 day period), the single-species treatments at mid shore increased in size and weight by approx 2mm and 0.15g These values are quite comparable with data for L.obtusata growth rates described by other workers.

After 117 days the amount and rate of increase had decreased rapidly. Shell size was increasing at two-thirds the previous rate. As the season extended through to the winter months, so the growth rate of L.obtusata decreased. This seasonal decrease in growth was noted by Hollingworth (1981) who stated that L.obtusata juveniles grew steadily until spring, then grew rapidly until late summer/autumn when they reached approx 10-11mm and growth slowed down for the winter. A similar pattern was also noted by Wright (1976), Guiterman (1970) and Goodwin (1975).

The changing growth rates can be related to the population dynamics of L.obtusata, which are well documented and have been investigated in this study (see Chapter 5). The population can be split into two components for the majority of the year (Goodwin 1978). There is a stable adult component; and an immature component of growing winkles. Briefly, when the peak of egg mass hatchings takes place, there is a third component to the population, which is the recently hatched component. The population soon returns to being composed of two components when the immature juveniles join the adult population and the recent hatchings join the immature

component. Winkles that hatch in spring/ winter of year one grow through the spring/summer to approximately 10-11mm by the end of their first year. After a quiescence in growth over the winter the winkles start growing again, and approach maturity above 10mm. By the summer of the second year the winkles are sexually mature. Growth follows a similar pattern in the second year (Wright 1976) but is slower, the winkles only growing approximately 4-5mm in this year; in the third year there is little if any growth. Most authors assume a longevity of 2-3 years (Wright 1976, Goodwin 1975) although others suggest 3-4 years (Hollingworth 1981, Daguzan 1976). The decrease in growth rate seen in the present study is, therefore, a response to the season: L.obtusata grows rapidly over the summer months and the rate of growth decreases in the winter. The decrease in growth in the winter has been attributed by many authors to a decrease in temperature which affects feeding rates (Wright 1976, Goodwin 1975). It may also relate in older animals to the development of gonads and spawning preparation. Goodwin (1975) believed that the reduced growth rates were due to sexual development which, in L.obtusata takes place at 10-12mm.

A similar pattern is seen for L.mariae at low shore, living on F.serratus in single-species stands. During the summer months L.mariae increased in size, as with L.obtusata this growth rate decreased during the winter season: growth rate as measured by shell size was only 40% of that in summer, and growth rate as measured by total weight was only 50% of the summer rate. There is no other work with which to compare the rate of growth of L.mariae.

Results from this study (see Chapter 5) suggest that L.mariae is an annual and hence its life cycle is different to that of L.obtusata. L.mariae grows rapidly from its hatching to reach adult size and sexual maturity (reached at 8-10mm, Goodwin 1975) by the first winter. It appears that not many animals actually survive to live for another year. Some do survive; but their life expectancy is, in contrast to L.obtusata, only 1-2 years. The winter decrease in growth rates does not necessarily represent a winter growth quiescence. It is more likely that this approaches the asymptote of growth for the animal's life, brought about by the winter season. At this size L.mariae has little growth potential to achieve as animals of this size are all sexually mature. This may explain the more severe growth decrease of L.mariae as compared to L.obtusata.

For L.obtusata there does not appear to be any biotic factor limiting growth in the winter months, since there appear to be large amounts of food available. It is possible, in the case of L.mariae, that food is limiting; either due to the seasonal nature of epiphyte resources, or due to the die-back of F.serratus (see Chapter 5). In the cages, however, macro-algae were not limiting and it is probable that the limiting factor was the time of year for both species. This may have caused a behavioural decrease in activity/growth; or perhaps the environmental aspects of winter (decreases in temperatures; increases in storm damage etc) caused a reduction in growth in the case of L.obtusata and the onset of maturity in L.mariae.

The animals transplanted to the other species' optimum level also exhibited a seasonal trend in growth

although there were differences in the rates of growth between the treatments. L.obtusata grew significantly better at low shore on F.serratus than it did on Ascophyllum at mid shore. The shell growth rate was approx 30% higher in the summer at low shore than at mid shore, and the increase in weight was approx 40% higher. This represents a great increase in growth as compared to mid shore. During the period between 56 and 117 days, however, the winter set in and the growth rates for both shell size and weight decreased to match those for the mid shore winkles. Although the winkles at low shore were larger and heavier after 117 days than mid-shore winkles they had still been influenced by the limiting factor introduced with the onset of winter, and their growth rates were therefore accordingly reduced to equal those of the mid shore winkles. The advantage that was presented by being at low shore as opposed to mid shore was therefore effectively removed in the winter months.

There are several possible explanations for the advantage that being caged at low shore gave to L.obtusata. Firstly, being at low shore results in a decrease in time spent exposed to air, and more time spent underwater (in this case not exposed to predators). L.obtusata at mid shore is not very active when exposed to air; as Ascophyllum becomes desiccated, L.obtusata crawls into the centre of the weed clump and settles there (Wright 1976; Bray 1974; Watson 1983 and pers obs.). At mid shore this represents a large period of time when the animal is not feeding. Being lower on the shore therefore increases the feeding time of L.obtusata as the weed is covered for long

periods of time during which it can graze. When it is uncovered it is only out of the water briefly, and therefore desiccation problems are lessened. The other main difference between the mid and low shore sites is the algal species on which the winkles are living. It is possible that F.serratus is energetically a more profitable alga for L.obtusata to graze on. As mentioned L.obtusata rips holes out of the fronds of F.serratus, the thallus of this species being almost a 2-D structure. This affect is shown in Plate 6.2. Ascophyllum is a more 3-D plant and although L.obtusata actually grazes into the weed it rarely forms a hole through the frond. Structurally F.serratus may be a simpler food source to graze. Watson (1983) has looked closely at the relationship between L.obtusata and fucoid algae. He suggested that the alga's physical structure may often inhibit grazing. In laboratory experiments Ascophyllum was shown to be far more resistant to abrasion than F.serratus. In a palatability test F.serratus was preferred to Ascophyllum by L.obtusata when compared to a control alga. It appears that F.serratus is easier to eat and is therefore chosen more readily than Ascophyllum. The chemical composition of the plant is very different to F.serratus, Ascophyllum being full of secondary plant compounds presumed to be noxious to grazers (Geiselman and McConnell 1981); F.serratus may therefore represent a more appetizing meal. Despite this, L.obtusata has a very strong attraction for the exudates of Ascophyllum (Watson 1983), possibly influencing the species' zonation (see Chapter 4).

Transplantation of L.mariae from low shore to mid

shore (from F.serratus to Ascophyllum) had a negative effect on the performance of this species, many individuals being found dead in the bottom of the cages. L.mariae grew less well at mid shore, its shell size growing at 60% the rate of the low shore site and its weight increasing by slightly less than this (40%) after 56 days. Unlike L.obtusata there was still a difference between the heights after 117 days. The rate of shell growth was quite similar between the two shore heights, decreasing from the summer growth by 70%. The increase in weight of the winkles decreased by less for the low shore site than the mid shore site after 117 days. The mid shore site's rate of increase being half that of the low shore. For both treatments this represented a winter decrease after the summer's growth.

The poor growth of L.mariae at mid shore can be attributed to a number of factors. Firstly, there is the difference in tidal height and resulting increase in emersion:immersion ratio which may affect the animals' behaviour and feeding rates. This does not, however, seem to inhibit L.mariae. As previously noted, L.mariae remains active at low water when uncovered (Sacchi 1967, pers obs). The greater exposure to air and increased desiccation may inhibit growth. In laboratory tolerance experiments L.mariae has been shown to be more susceptible to extremes of temperature and desiccation than L.obtusata (Sacchi 1972a and b). This could prevent the winkle from effectively grazing. In fact the most likely explanation for L.mariae's poor growth is food related. Ascophyllum is a very tough and unpalatable weed (Watson 1983) as compared with F.serratus. There is evidence (see Chapter 4 and

Watson and Norton 1987) to suggest that L.mariae is a micro algal grazer, browsing over the surface of F.serratus and eating epiphytic microalgae and detritus which are plentiful (Round 1984). In contrast Ascophyllum is documented as having only Polysiphonia as a common epiphyte (Round 1984) and also has many inhibitory chemicals to influence fouling and grazing (Hornsey and Hide 1974, 1976). Ascophyllum has been shown to shed its epidermis regularly (Filion-Myklebust and Norton 1981) thereby removing any epiphytes present. Watson (1983) suggested that L.mariae's buccal musculature was too small to allow penetration of the abrasion-resistant Ascophyllum. At mid shore, therefore, L.mariae is exposed to a well-defended and relatively unpalatable macroalga on which very few of its food source, microalgae, are found. The decreased rates of growth could be attributed to the limiting amounts of food that can be grazed from the Ascophyllum fronds and to possibly limiting abiotic factors.

The mixed treatments where equal numbers of L.obtusata and L.mariae were enclosed at the different tidal levels showed very interesting results, although they proved to be statistically unimportant in affecting the winkles growth rates. At both mid shore and low shore L.obtusata grew better after 56 days in the mixed treatments than in the single-species treatments. Towards the winter season the growth rates were very similar and no difference was seen between the treatments. For L.mariae the picture is different. L.mariae appeared to grow better in the absence of L.obtusata although this was less clear cut. After 56 days there was no difference in the rate of

weight increase between mixed and single species treatments at either tidal height. For shell size L.mariae increased slightly faster in single species stands at low shore and mixed stands at mid shore. After 117 days the rate of weight increase was identical between the treatments at mid shore, but at low shore the presence of L.obtusata appeared to decrease the rate of L.mariae weight increase. For the shell size the difference was slight although the same trend was prevalent for the mid shore site. It is possible that if the cages were set up earlier in the year L.obtusata would deplete the low shore cages of algae and hence leave L.mariae with a limiting surface area off which to browse epiphytes. The poor quality of the F.serratus in cages containing L.obtusata at the end of the experiment pointed towards such an interaction.

6.4.3 CONCLUSION

The results from these experiments allow some inferences about the niche dimensions of the two species to be made. In the case of L.mariae it seems that mid shore is outside the potential niche of the species as dictated by physical factors. Therefore the species is restricted to those areas of the shore that are within the species' potential niche, and this is the low shore area. This is the species' realized niche, and as shown by the vertical height transects (see Chapter 4) it is a much narrower niche than that of L.obtusata.

In these experiments the potential niche of L.obtusata was shown to be much wider than the area occupied in the vertical height transects. If L.obtusata

does so much better at low shore than on the mid-shore, it is appropriate to ask why it does not live there, or at least migrate there to feed. There are a number of possible explanations. Firstly, at low shore there is an increased pressure from predation because of longer exposure to marine predators. In the case of crab attack L.obtusata is less well structurally defended than L.mariae (Reimchen 1982). In the cages, predators were effectively excluded. Further work along the methods of Seeley (1986) could elucidate whether predation affected zonation of L.obtusata and this is investigated in Chapter 8. Secondly, for a long-lived species such as L.obtusata, F.serratus is not a reliable food source to exploit. It does not form the dense beds that Ascophyllum does and is also shorter lived and more variable, being subject to defoliation (Knight and Parke 1950) and storm damage. If large populations of L.obtusata were to graze at low shore on F.serratus then they would soon deplete the resource; as shown by their denudation of weed in low shore cages. Such a strategy would be extremely unstable from an evolutionary stand point. Behavioural investigations support this theory: uncaged L.obtusata transplanted down shore migrate upshore (see Chapter 7). Laboratory experiments by Watson and Norton (1987) show L.obtusata to be attracted to Ascophyllum over any other algae. Therefore the behaviour of the species reinforces the suitability of mid shore as opposed to low shore.

7. MOVEMENT

7.1 INTRODUCTION

The zonation patterns of intertidal species are governed by numerous abiotic and biotic factors. In the case of sessile species abiotic tolerances have been shown to be of primary importance (Connell 1961). The maintenance of intertidal zonation patterns of mobile species has often been explained by behavioural responses to environmental cues (Gendron 1977, Underwood 1979, Petraitis 1982). The basic premise of these explanations is that mobile species are behaviourally "programmed" to respond, via movement, to maintain their "optimum" position on the shore. This behavioural programme is thought to be manifest in the taxes shown by species to various environmental stimuli. These taxes are also thought to aid displaced animals to return to their optimum position on the shore: displaced individuals of some species are able to return to their original home ranges, presumably via orientation to environmental cues.

Intertidal gastropods have been shown to respond to a number of different environmental cues. The most common are light (Burdon-Jones and Charles 1959; Charles 1961a , b and c; Newell 1958 a and b; Fraenkel 1927; Evans 1961,1965); and gravity (Neale 1965; Gowanloch and Hayes 1926, Underwood 1972). Gravity effects are often linked with phototaxis (Fraenkel 1927; Evans 1961, 1965). The effect of tidal rhythms has also been linked with photo- and geo-taxis (Underwood 1972 a and b; Petpiroon and Morgan 1983; and Zann 1973). The literature on this subject is

often inconclusive and confusing (see review by Underwood 1979). Relating the simple responses seen in laboratory conditions to field situations is often misleading. The elimination of all other cues available on the shore will deprive the experimental animal of natural conditions and therefore any movement patterns seen will probably not resemble in situ movement. The importance of these controlling taxes remains to be verified conclusively in the field and the taxes described probably represent single pieces of a behavioural jigsaw puzzle.

The taxes of L.obtusata have been investigated (often as the species L.littoralis) prior to its division into two species. These studies attempted to relate the maintenance of the zone inhabited by the species to it's responses to light and gravity (Janssen 1960; Evans 1965; Von Dongen 1956; Charles 1961; Barkmann 1955). The results were varied and confusing. The most important taxis that all the workers noted was the attraction of the "species" for fucoid algae. The flat winkle was shown to be attracted to algae from up to a metre away (Van Dongen 1956), and to zone in tidal tanks only in the presence of fucoids (Underwood 1972a; Thompson 1968; Evans 1965). There was much conflict between different workers concerning the relative attraction of different fucoid species. As Underwood (1972a) pointed out this was probably due to the use of different varieties (colour morphs) by various workers. With hindsight this can be attributed to the inclusion of L.mariae with the L.obtusata samples. It is interesting to note that often the differences between the colour morphs olivacea (- L.obtusata) and citrina (-

L.mariae) match observed differences between the two species L.obtusata/mariae. For example the two showed behavioural differences when immersed (Barkmann 1955); and different algal preferences (Van Dongen 1956). This type of work has been more rigorously carried out by Guiterman (1970) who recognized both L.obtusata and L.mariae. He clarified a number of the inconsistencies of previous workers and described L.obtusata as being principally negatively geotactic and negatively phototactic, and having strong attractions to fucoids. He also explained the difference in behaviour between the two species: L.obtusata being principally negatively phototactic and therefore retreating into the weed mass when exposed; and L.mariae, not being as strongly negatively phototactic as L.obtusata, and hence actively crawling over the surface of the weed when exposed. Apart from this work little has been done to compare the responses of the two species in the field either at their normal zones or when displaced to the other species shore level.

Similar behavioural responses of individuals of other species have been examined after displacement in the field. Experimentally displaced animals have been shown to move towards their home zone (Gendron 1977; McQuaid 1981; Petraitis 1982; Doering and Phillips 1983; Thain, Thain and Kitching 1985; Bovbjerg 1984). These sorts of experiments attempted to investigate the effect on movement of the complete range of environmental cues, and to decide which are the most important. Such experiments are difficult to interpret and investigate rigidly (as discussed by Chapman and Underwood, 1985, and Chapman, 1986). Despite this

they are perhaps of more value than laboratory investigations on single taxes.

The zonation patterns of mobile species can be analyzed on three levels according to Bovjberg (1984):

"(1) The immediate cause is habitat selection at any stage of the life cycle and this level has a strong behavioural component of perception and response.

(2) The ecological cause has a strong physiological component over ecological time; the needs and the tolerance ranges of the species define the local optimum, the framework within which habitat selection operates.

(3) The ultimate cause is evolution, the selective forces moulding the species over its entire range over geological time."

The first point describes the importance of behavioural responses to environmental cues as previously discussed. The second point concerns habitat selection and the importance of physiological tolerances (responses to the abiotic environment). This is not the only important factor, since escapes from competition or predation in response to the biotic environment will be equally as important. The third point illustrates the importance of evolution as a selective agent, either driving to keep the species at its optimum zone or selecting for responses to return it to its zone when displaced.

The clear zonation of L.obtusata and L.mariae presumably illustrates points (1) and (2). Overlap between the zones of the two species on sheltered shores is rarely seen, usually being due to storm action (pers.obs). The response to this displacement is of great interest as it

results in the maintenance of the species' respective zones. Do the winkles, when displaced, home to their specific zones? If so evolution has selected for maintenance of that shore level, and the next question should be what has driven this selection? The subsequent movement of displaced winkles may shed light on the vertical partitioning of the niches of these two species. It may also allow the relative importance of selective forces on the two species in evolutionary time to be elucidated.

7.2 MATERIALS AND METHODS

The aims of the experimental work can be divided into two: firstly to investigate the movement of winkles in their home zones; and secondly the movement of winkles displaced from their home zone to the preferred zone of the other species. The techniques employed for the two investigations were similar and can be described under the one section. All the experiments were carried out at Sawdern at West Wales, during March, 1987.

Adult winkles, as denoted by thickening of the aperture lip (Goodwin and Fish 1977), were selected from the appropriate shore level. Therefore L.obtusata (size range 14-17mm) was collected from mid shore; and L.mariae (size range 8-12mm) was collected from low shore. The exact heights from which the winkles were removed and at which the experiments were carried out were based on the fixed points previously surveyed for the vertical height and population studies (see Chapters 4 and 5). Care was taken not to select any individuals which were obviously parasitized (parasitized individuals have "giant" shells and in some species infection has been shown to affect movement-Williams and Ellis 1975). The winkles collected were measured, to an accuracy of 0.05mm, using vernier calipers, and individually numbered. The numbers used were "Micromarkers" (W.H.Brady and Co Ltd, as used by Olafson 1986). These were stuck to the shell using Super Glue (Loctite).

The experimental design involved 4 treatments. Two of these used L.obtusata at their home range (mid shore)

and L.mariae at their home range (low shore). These treatments investigated the normal movement of the two species at their respective tidal heights and also provided controls for movement initiated by handling and displacement effects. The second two treatments were of winkles moved to the shore level appropriate to to the other species; L.obtusata transplanted to low shore and L.mariae transplanted to mid shore. These treatments investigated the effect of displacement from their normal range on the winkles' movement.

These treatments were replicated at different parts of the shore to avoid simple pseudoreplication (Hurlbert 1974). In each replicate 30 individuals of each species were used. This number was chosen using the results of a previous pilot experiment which suggested that n=30 would ensure a sufficient recapture to give a statistically valid sample. The experimental design is illustrated in Table 7.1. All the winkles used in the experiments were handled in the same way prior to replacement onto the weed. Any possible disturbance effects were therefore similar for all the treatments.

On the shore 4 sites were chosen which had similar algal cover and uniform slopes. Two of these were at low shore, with a cover of F.serratus; and two at mid shore with a cover of Ascophyllum. At these sites the respective experimental animals were released. The animals were released by placing them at 5cm intervals in a grid which was orientated to two fixed points on the shore. The fixed points were two bolts screwed into the substrate. These two fixed points were placed parallel to the slope of the

Table 7.1

Experimental Design for the movement experiment.

	MID SHORE		
SITE 1	30 *L.obtusata*	30 *L.mariae*	= 60
SITE 2	30 *L.obtusata*	30 *L.mariae*	= 60
	LOW SHORE		
SITE 3	30 *L.obtusata*	30 *L.mariae*	= 60
SITE 4	30 *L.obtusata*	30 *L.mariae*	= 60
	120	120	240

shore at a known distance apart. The compass bearing relative to magnetic north was taken from these two points and corrected to true north using an Ordnance Survey map. The two species were released one at each side of the line between the two fixed points and within 1 metre of each other. The exact position of each individual was known at the start of the experiment. All calculations of movement were made from these reference bolts using coordinate geometry following the methods of Underwood (1977). This required the scoring of a measurement from each bolt to the winkle to be recorded. As the distance between the bolts was a known constant the direction and distance of movement of the winkle could be calculated from the two sets of points.

Movement was estimated during emersion periods and was scored after 1 (24 hours),2 and 4 days. Due to the nature of the substrate, and L.obtusata's behaviour of crawling into the weed mass, individuals had to be searched for extensively. As a result of this the winkles' movement was scored to the nearest 5cm as searching often slightly displaced the individuals.

The movements of the winkles can be divided into the DISTANCE travelled and the DIRECTION of this movement. The distance moved was calculated using coordinate geometry and the direction was scored as angular bearings relative to North. The approximate direction of the slope of the shore was also measured by surveying the experimental areas.

ANALYSIS

The measurements were analyzed by a BASIC computer

programme which calculated the distance moved by an individual from the initial release point to the next point and the direction of this movement. From these data circular statistics, the mean resultant vector and mean angle, were calculated following the methods of Zar (1974). The direction was examined using Rayleigh's Test to see whether the direction of movement was random or not. A significant result indicated that movement was not random but directional.

The distance moved was analyzed by a 3 Factor Analysis of Variance. The data were transformed by natural logs to eliminate the linear relationship found between the mean and S.D. of the samples (see Elliot 1977 and Underwood 1981 for discussion). Significant differences between the means were examined using Scheffes Test (Zar 1974).

7.3 MOVEMENT RESULTS

7.3.1 DIRECTION OF MOVEMENTS

The hypothesis examined by Rayleigh's Test is that the direction of movement shown by the populations sampled is random. A significant result indicates directional movement. The results of the Rayleigh Test are shown in Tables 7.2-7.4 along with the calculated mean directions and mean resultant vectors (r). These results illustrate that many of the treatments showed non-random movement. The direction of movement of individual winkles are illustrated in Figures 7.1-7.3.

MID SHORE

After day one both sets of transplanted L.mariae showed non-random movement in a downshore direction. This continued for both the second and fourth days' readings. Throughout the experiment all the L.mariae treatments transplanted to mid shore showed a non-random movement downshore. The directions of movement of L.obtusata retained at mid shore, the control winkles, were not as uniform. In one of the replicate areas, Site 1, L.obtusata showed random directions of movement for all three days. At site 2, however, non-random directions of movement were recorded for days one and two. This direction was constant for both days at 248°, which was in a slightly downshore direction. After four days, however, this control sample showed a random orientation of movement, in a similar fashion to the first replicate area.

LOW SHORE

At low shore the control winkles were L.mariae,

Table 7.2
Mean angle, mean resultant vectors and Rayleigh's Z for the directions moved by by littorinids on day 1 of the experiment.

			DAY 1 Mean Resultant Vector	Z	Mean Angle	Significance
MID SHORE						
SITE 1	L.obtusata	(C)	0.147	0.259	28	N.S.
	L.mariae	(T)	0.713	7.63	185	* * *
SITE 2	L.obtusata	(C)	0.688	7.57	248	* * *
	L.mariae	(T)	0.757	9.17	233	* * *
LOW SHORE						
SITE 3	L.obtusata	(T)	0.635	7.66	262	* * *
	L.mariae	(C)	0.256	1.11	97	N.S.
SITE 4	L.obtusata	(T)	0.342	2.57	330	N.S.
	L.mariae	(C)	0.334	2.12	275	N.S.

KEY
C = control; T = treatment
* * * = direction of movements significantly differs from being random at the 0.01 level
N.S = random direction of movement is not disproved

SLOPE OF SHORE

SITE 1	Upshore approx.	360	SITE 2	Upshore approx.	360
	Downshore approx.	180		Downshore approx.	220
SITE 3	Upshore approx.	360	SITE 4	Upshore approx.	360
	Downshore approx.	180		Downshore approx.	240

Table 7.3
Mean angle, mean resultant vectors and Rayleigh's Z for the directions moved by littorinids on Day 2 of the experiment.

			DAY 2 Mean Resultant Vector	Z	Mean Angle	Significance
MID SHORE						
SITE 1	L.obtusata	(C)	0.349	1.46	178	N.S.
	L.mariae	(T)	0.548	6.01	193	* *
SITE 2	L.obtusata	(C)	0.826	11.6	248	* * *
	L.mariae	(T)	0.487	4.27	228	*
LOW SHORE						
SITE 3	L.obtusata	(C)	0.624	6.62	297	* * *
	L.mariae	(T)	0.365	2.42	11	N.S.
SITE 4	L.obtusata	(C)	0.532	4.53	355	*
	L.mariae	(T)	0.351	2.34	17	N.S.

KEY
C = control; T = treatment
* = direction of movement significantly differs from being random at the 0.05 level
* * = 0.01 level
* * * = 0.001 level
N.S. = random direction of movement is not disproved

SLOPE OF SHORE

SITE 1	Upshore approx. 360	SITE 2	Upshore approx.	360
	Downshore approx. 180		Downshore approx.	220
SITE 3	Upshore approx. 360	SITE 4	Upshore approx.	360
	Downshore approx. 180		Downshore approx.	240

Table 7.4
Mean angle, mean resultant vectors and Rayleigh's Z for the directions moved by littorinids on the day 4 of the experiment.

			DAY 4 Mean Resultant Vector	Z	Mean Angle	Significance
MID SHORE						
SITE 1	L.obtusata	(C)	0.426	2.18	293	N.S.
	L.mariae	(T)	0.932	11.3	188	* * *
SITE 2	L.obtusata	(C)	0.358	1.15	306	N.S.
	L.mariae	(T)	0.713	5.08	240	* *
LOW SHORE						
SITE 3	L.obtusata	(T)	0.916	11.75	344	* * *
	L.mariae	(C)	0.331	1.21	3	N.S.
SITE 4	L.obtusata	(T)	0.865	8.98	338	* * *
	L.mariae	(C)	0.491	2.65	357	N.S.

KEY
C = control; T = treatment
* * = direction of movement significantly differs from being random at the 0.01
* * * = 0.001
N.S. = random direction of movement is not disproved

SLOPE OF SHORE

SITE 1	Upshore approx.	360	SITE 2	Upshore approx.	360
	Downshore approx.	180		Downshore approx.	220
SITE 3	Upshore approx.	360	SITE 4	Upshore approx.	360
	Downshore approx.	180		Downshore approx.	240

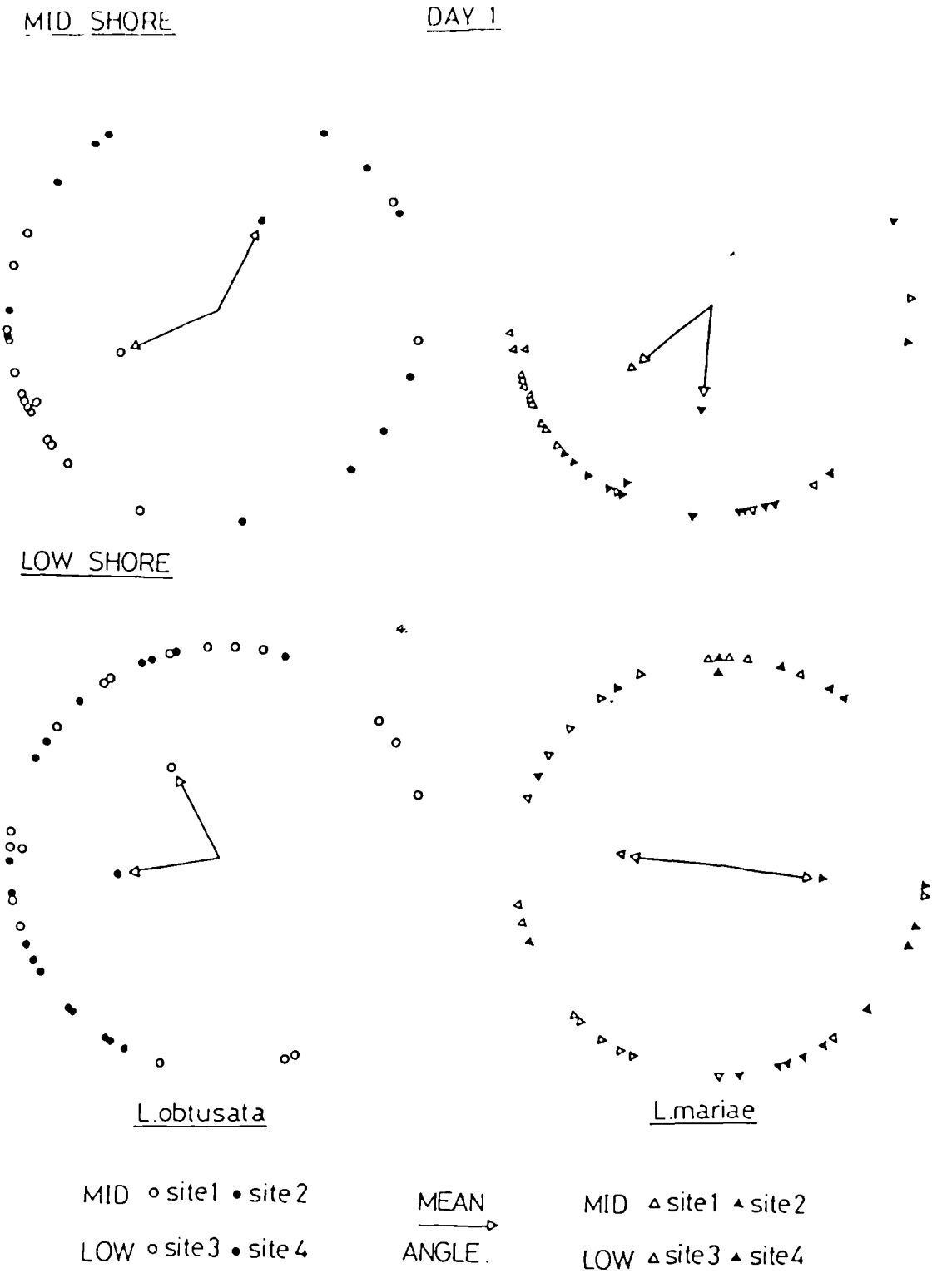


Figure 7.1
Directions of movements of individual littorinids after Day One.

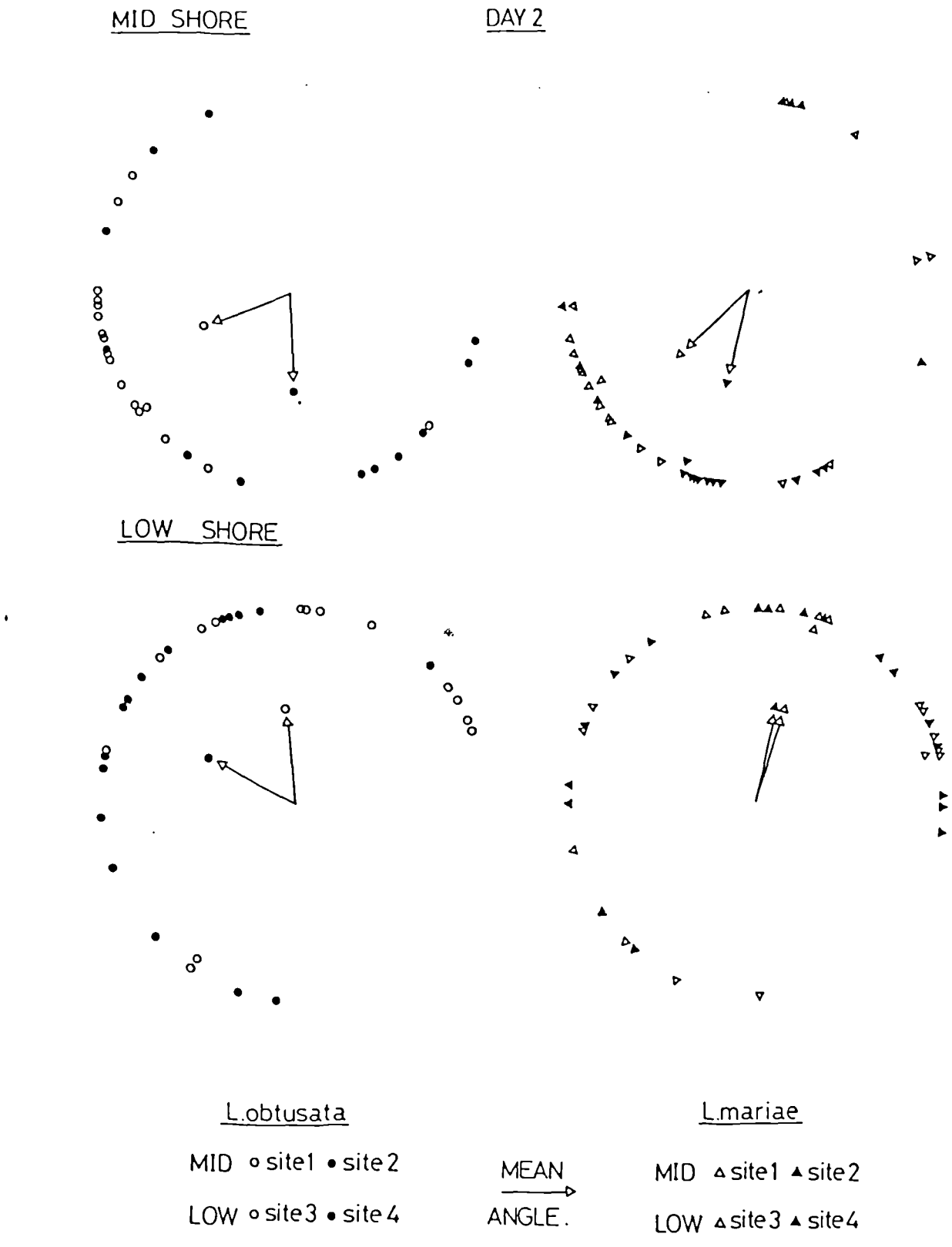


Figure 7.2
Directions of movements of individual littorinids after Day Two.

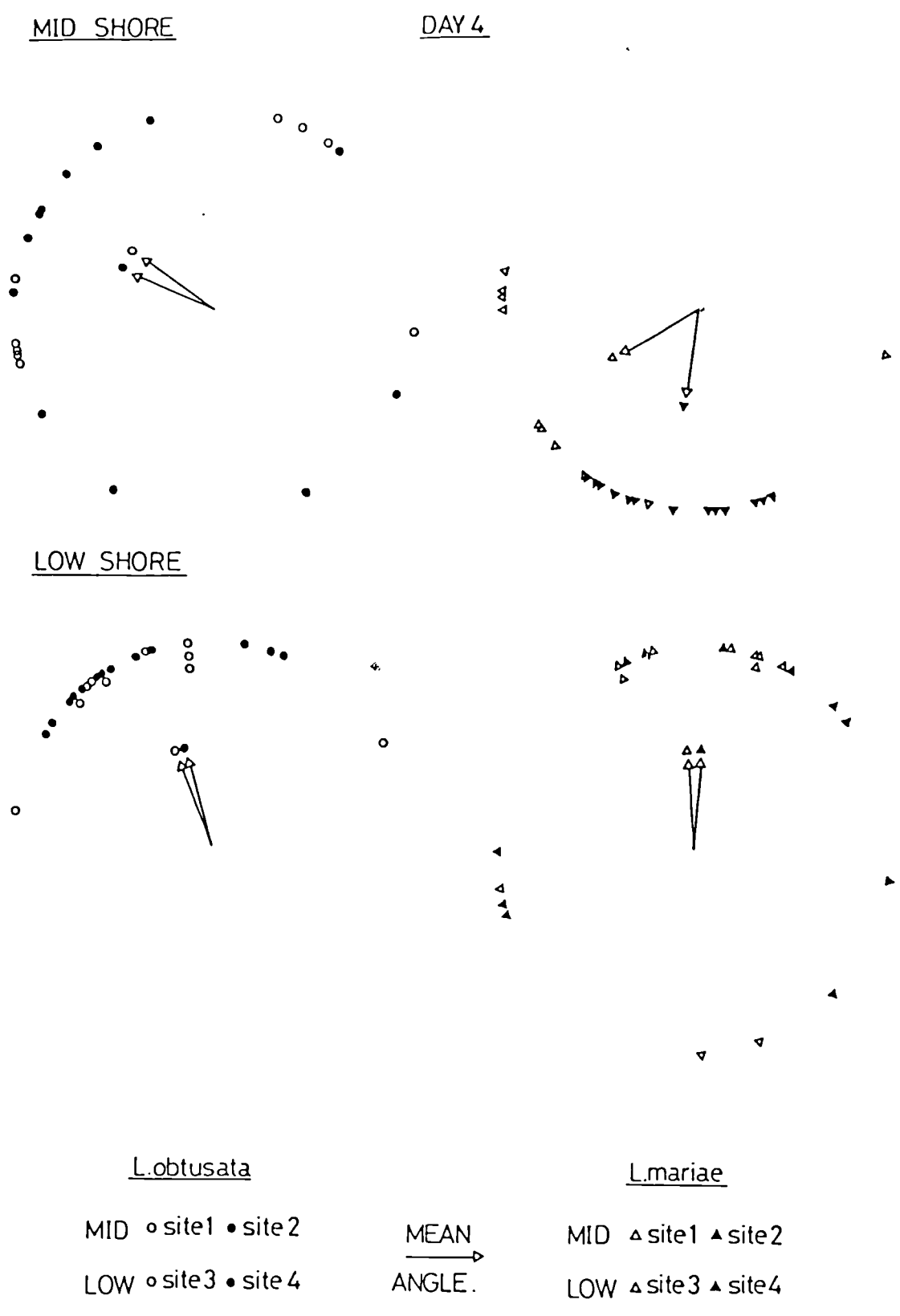


Figure 7.3
Directions of movement of individual littorinids after Day Four.

translocated at their own shore level. The treatment winkles were L.obtusata transplanted from mid shore. For all the days recorded L.mariae showed a random direction of movement (the null hypothesis of the Rayleigh Test was not disproved). The transplanted L.obtusata at site 4 showed a significant, non-random, orientation of movement upshore for all the days recorded. At site 3 L.obtusata showed random movement after one day but after two and four days showed non-random movement, again in an upshore direction.

Therefore after four days all the transplanted animals showed non-random movement in the direction of their home zone. All the control animals, at their correct shore levels, exhibited random directions of movement. This pattern developed as the experiment continued, the initial discrepancies possibly being due to a period of adjustment and re-orientation after setting up the experiment.

7.3.2 DISTANCE MOVED

The results from Three Way Analysis of Variance to compare the distances moved during the different treatments of the experiment are shown in Tables 7.5-7.7. These show that there were significant differences in the distances moved by the winkles in the experiment. After one day there were significant differences between the shore heights; the replicate areas and the interaction terms of height, species and area. After two days the same factors, except for the three way interaction factor, were significant. By day four only the height and the height/species interaction showed significantly different distances of movement. Reference to the cell mean values

Table 7.5
Three Way Analysis of Variance to investigate the distances moved after day 1. The significant results of Scheffe's Test are shown at the bottom of the ANOVA table.

SOURCE OF VARIATION	DF	MEAN SQ	F	SIGNIFICANCE
SPECIES	1	0.132	0.304	N.S.
HEIGHT	1	28.82	66.71	* * *
AREA	1	9.987	23.12	* * *
SPECIES X HEIGHT	1	5.854	13.55	* * *
SPECIES X AREA	1	5.283	12.23	* * *
HEIGHT X AREA	1	3.273	7.576	* * *
SPECIES X HEIGHT X AREA	1	1.999	4.626	* * *
RESIDUAL	129	0.432		

KEY
* * * = significant at the 0.001 level
N.S. = not significant

SCHEFFE'S TEST

L.mariae sites 1 and 2> L.obtusata at sites 1, 3 and 4

> L.mariae at site 3

L.mariae site 2 > L.mariae at site 4

L.obtusata site 2 > L.obtusata at site 1,3 and 4

> L.mariae at site 3 and 4

Table 7.6
Three Way Analysis of Variance to investigate the distances moved after day 2. The significant results of Scheffe's Test are shown at the bottom of the ANOVA table.

SOURCE OF VARIATION	DF	MEAN SQ	F	SIGNIFICANCE
SPECIES	1	0.870	1.762	N.S.
HEIGHT	1	30.82	62.44	* * *
AREA	1	4.136	8.381	* * *
SPECIES X HEIGHT	1	7.743	15.69	* * *
SPECIES X AREA	1	6.409	12.99	* * *
HEIGHT X AREA	1	2.987	6.053	* * *
SPECIES X HEIGHT X AREA	1	0.687	1.393	N.S.
RESIDUAL	129	0.493		

KEY
* * * = significant at the 0.01 level
N.S. = not significant

SCHEFFE'S TEST

L.mariae sites 1 and 2 > L.obtusata at sites 1 and 3
> L.mariae at site 3 and 4

L.obtusata site 2 > L.obtusata at site 1,3 and 4
> L.mariae at site 4

Table 7.7
Three Way Analysis of Variance to investigate the distances moved after day 4. The significant results of Scheffe's Test are shown at the bottom of the ANOVA table.

SOURCE OF VARIATION	DF	MEAN SQ	F	SIGNIFICANCE
SPECIES	1	0.347	0.679	N.S.
HEIGHT	1	2.229	4.367	*
AREA	1	0.336	0.659	N.S.
SPECIES X HEIGHT	1	7.431	14.56	* * *
SPECIES X AREA	1	2.001	3.922	N.S.
HEIGHT X AREA	1	0.768	1.506	N.S.
SPECIES X HEIGHT X AREA	1	0.491	0.962	N.S.
RESIDUAL	129	0.510		

KEY
* = significant at the 0.05 level
* * * = significant at the 0.001 level
N.S. = not significant

SCHEFFE'S TEST

L.mariae site 1 > L.obtusata at site 1

(see Table 7.8) showed that winkles moved further at mid shore, and those at site 2 moved the greatest distance.

These results were further analyzed by comparing the mean values for each treatment with all the other treatments using Scheffe's Test. The results for this are shown at the bottom of Tables 7.5-7.7. These show that for day one L.mariae at sites 1 and 2 (at mid shore) moved significantly further than L.obtusata at site 1, site 3 and site 4; and than L.mariae at site 3. L.mariae at site 2 also moved further than L.mariae at site 4. L.obtusata at site 2 moved a significantly greater distance than all the other treatments, apart from L.mariae at mid shore. On day 2 a similar pattern was seen; both mid shore, displaced, L.mariae treatments moved significantly further than the low shore L.mariae and than L.obtusata at site's 1 and 4. L.obtusata at site 2 again moved a significantly greater distance than any other treatment of L.obtusata and than L.mariae at site 4. After four days there was only one significant difference in the distance travelled by the treatments: at site 1 L.mariae moved further than L.obtusata.

It can be concluded, therefore, that winkles at mid shore generally moved further than those at low shore, and this was especially true of L.mariae which were moving towards their home zone. L.mariae in general moved further than L.obtusata. L.obtusata moved a similar distance in all the treatments, except at site 2 where individuals moved a lot further. This variation in L.obtusata possibly reflected a difference between the replicate areas. After 4 days these differences were less pronounced.

Table 7.8
Mean, standard deviation and sample size of distances moved by littorinids during the experiment.

TREATMENT	DAY 1	DAY 2	DAY 4
MID SHORE			
SITE 1			
L.ob	24.1±13.7(12)	31.2±15.8(12)	48.9±29.4(12)
L.ma	79.2±29.6(15)	106.6±44.4(20)	123.4±39.7(13)
SITE 2			
L.ob	120.1±56.8(16)	119.7±53.9(17)	92.5±43.0(9)
L.ma	120.2±64.4(15)	135.4±68.8(18)	128.6±89.3(10)
LOW SHORE			
SITE 3			
L.ob	28.1±16.4(19)	46.0±41.3(17)	83.6±51.3(14)
L.ma	24.7±14.6(17)	36.9±19.2(18)	66.9±56.3(11)
SITE 4			
L.ob	44.5±23.6(22)	56.5±33.4(16)	80.6±33.9(12)
L.mar	25.7±10.5(19)	33.2±21.7(19)	49.9±26.1(11)

KEY
L.ob = L.obtusata
L.ma = L.mariae

7.4 DISCUSSION

The results of the movement experiments showed that L.obtusata and L.mariae made non-random movement towards their home zones when displaced to the shore level normally occupied by the other species. The two species at their respective shore levels showed a random direction of movement after an initial settling period. This pattern was most clearly seen after four days movement. After one day the pattern was confused but after two days became more clear. Initial movement may have been the result of disturbance factors due to the effect of displacement and marking, a phenomenon which has been noted by other workers (Underwood and Chapman 1985; Chapman 1986 and Petraitis 1982). An improved response with time has also been recorded for L.littorea after an initial settling phase (Alexander 1960 and Gendron 1977).

The distances moved by winkles also showed a change during the duration of the experiment. After one and two days the winkles at mid shore moved further than those at low shore. This was especially true of L.mariae. There was some variation between the sites at mid shore, winkles at site 1 moving further than those at site 2, and this difference was more accentuated for L.obtusata. After 4 days there was very little difference between the distances moved in any of the treatments; the only significant difference was between L.mariae and L.obtusata at site 1.

There are a number of explanations for this discrepancy in the distances moved by the winkles after different treatments. Firstly, as the majority of the

differences were seen only in the first two days it is possible that distances moved, as well as the directions (noted above) were related to the effects of displacement. After four days the displacement effect would be less dramatic and hence few differences were seen. At this time, however, all the winkles displaced from their home zones moved further than the controls. This was significant in only one case but represented a consistent trend, not in keeping with random displacement effects.

The increased movement of L.mariae at mid shore (i.e. displaced animals) after one and two days may be a reflection of differences between the behaviour of the two species, L.mariae showing increased movement at this level. If this hypothesis is correct then the pattern was masked by an anomalous reading for L.obtusata at site 2 which also moved a long way. Conversely it is possible that the differences can be explained by variation caused by the tidal height; both species moving further at mid shore. If this was the case then the short distance moved by L.obtusata at site 2 is an anomalous reading.

The differences between the species could be explained by the fact that L.mariae is generally more active than L.obtusata. When the winkles are emersed L.mariae continues to crawl over the surface of the algae whilst L.obtusata retreats into the algal mass. This difference in behaviour combined with the strong directionality of L.mariae's movement, will result in greater distances being moved by L.mariae as compared to L.obtusata.

The differences moved at mid shore as compared to

low shore may be due to a difference in the substrate over which movement took place. The distance moved would have been facilitated by the ease with which the winkles could move over the substrate, i.e. the algal cover. At mid shore this would be maximal when the algae were emersed, as the Ascophyllum fronds would cover approx. 90% of the rock surface and form a regular homogeneous carpet over which movement would be relatively easy. At low shore the winkles' substrate was F.serratus. This alga is far more patchy and irregular in distribution than Ascophyllum. At low water the stipes of F.serratus hold the fronds off the rock surface and would effectively make movement between plants more difficult for the winkles than at mid shore. Therefore movement between and within plants would be greater at mid shore on Ascophyllum. It should be noted that the majority of directional movement at mid shore probably took place at low water; or as soon as the alga was uncovered by the water. Movement in the horizontal plane would have been prevented at high water due to the fact that the alga floats vertically.

The variation in the distances moved can be explained by differences between the two winkle species and by differences in the effect of the habitat on ease of movement. This experiment did not clearly distinguish between the two, mainly because of variation between the replicate sites of L.obtusata at mid shore, which confused the distinction between the factors of height on shore and species. Very few authors have examined variation in distances moved between displaced animals and controls, most of the work concentrating on the direction of

movement. Some workers (Underwood 1977; Underwood and Chapman 1985; Chapman 1986) have examined distances moved but the results tend to be discussed in less detail than the directions moved.

The random direction of movement of the controls after 4 days illustrated a passive maintenance of shore zone by the species. Such random movement of species at their respective tidal level has been demonstrated in the field for Nerita atramentosa and Bembicium nanum (Underwood 1977); L.littorea (Alexander 1960; Gendron 1977; Petraitis 1982); and L.africana knysnaensis (McQuaid 1981). Very few authors have examined the movement of control animals at their respective tidal heights when investigating movement patterns of displaced animals (see Chapman 1986 for review) and the experimental design employed in this study was an improvement on many previous experiments. This experiment also had adequate replication of both blocks of the design (mid shore and low shore areas, replicated twice). The inadequecies of other designs are discussed by Chapman (1986) and Underwood and Chapman (1985). Unlike the findings of Petraitis (1982) the replicate areas in this experiment after four days yielded similar results for direction although the distances did vary. Petraitis found that his areas showed dissimilar directions of movement, but his areas were on separate beaches, not on separate areas of the same beach, as in the present study.

The displaced winkles in this experiment all showed directional movement towards their home zones after four days. As the environmental cues were similar for all the experimental animals this is a clear behavioural response

to regain a particular shore-level. It was not clear from this experiment what the cues for this directional movement were. Such homing behaviour in displaced gastropods has been noted by many authors : L.littorea (Alexander 1960; Petraitis 1982; Gendron 1972); Nodilittorina (Chen and Richardson 1987); Tegula funebralis (Byers and Mitton 1981; Doering and Phillips 1983); L.africana knysnaensis (McQuaid 1981); Nerita spp (Bovbjerg 1984); Gibbula umbilicalis (Thain et al 1985) and L.scutulata and L.planaxis (Bock and Johnson 1967). These movements have been described as the species responding behaviourally to maintain a specific set of environmental conditions; the species actively selecting their "preferred" habitat. The underlying premise is that each species performs optimally at its respective zone of the shore, and by being mobile is able to respond to displacement from this level. It has been shown (see Chapter 3) that L.obtusata and L.mariae are strongly zoned on sheltered shores. As they are both mobile species it can be assumed that their zonation is effected by behavioural responses and that evolution has selected for the development of these responses as a result of the suitability of the environment at this level. It has been noted that after storms L.obtusata is often displaced to low water. This is soon corrected as few L.obtusata are found at this level when the weather has become calm (pers. obs.)

This series of experiments has provided no evidence as to the cues that the winkle species used to orientate their behaviour. A single taxis is not sufficient to describe the movements shown by these species.

Undoubtedly a number of factors, as suggested by Underwood and Chapman (1985), combine to provide the stimuli to which the species responds in the way of directional movement. It seems likely that the presence/absence of preferred algal species is the most important cue, as these also reflect tidal level. This view has been suggested by many authors (Watson 1983; Watson and Norton 1987; Barkman 1955 ; Guiterman 1970; and Bray 1970). Underwood (1979) proposed that upward homing movement by herbivorous species was mediated by negative geotaxis until the species reached a preferred alga. Then the species would adopt random movement, grazing on this alga which effectively "overrides" the behavioural negative geotaxis. Laboratory based evidence to support this has been proposed by Guiterman (1970) and Underwood (1972a) who both showed L.obtusata to zone in tide tanks only in the presence of algae. To account for downshore homing movement,Underwood suggested that increased physiological intolerance upshore will orientate species back towards their home zones. These patterns would agree with the evidence available for L.obtusata and L.mariae but it has yet to be rigorously tested. The notable exception is work by Ebbenge-Wubben (quoted in Barkman 1955) which showed that if fucoid algae were removed from the shore L.littoralis (presumably L.obtusata) crawl above high water and die. This provided some field evidence for Underwood's proposal, and demonstrated the usefulness of field manipulations in this area.

The shore levels adopted by the two species presumably represent their optimum levels, or realized

niches. As previously noted in Chapter 4 the low shore area represents a physiological optimum for L.mariae. Subsequent movement upshore represents a departure from this optimum and presents physiological extremes of temperature and desiccation for the species. At these levels L.mariae is also removed from its host alga F.serratus and forced to live on Ascophyllum. L.mariae is repelled by extracts of Ascophyllum and is reluctant to feed on the alga (Watson 1983). L.mariae is a micro-algal grazer and probably suffers food limitation on Ascophyllum which has been recorded as having very few epiphytes, apart from Polysiphonia lanosa (Round 1984). Ascophyllum also sheds its epidermis frequently, thus preventing epiphyte loading (Filion-Myklebust and Norton 1981) and is extremely tough to penetrate and feed on (Watson 1983). As shown in the transplant cages at mid shore, L.mariae cannot tolerate the conditions at mid shore and either dies or its growth is inhibited. This transplantation to mid-shore therefore removes L.mariae from its potential niche, the niche that is dictated by physical factors. The driving selection force for L.mariae to home to low shore when displaced is therefore physiological. Selection, in an evolutionary sense, will favour those individuals which are able to maintain this zone, or which when displaced are able to regain this level by movement. Physiological tolerances set the upper limits of L.mariae's niche and the correct shore level is maintained by behavioural responses to displacement.

The situation is not as clear-cut for L.obtusata. L.obtusata homes to mid shore when displaced to low shore.

In previous experiments (Chapter 6) it was shown that when L.obtusata was transplanted to low shore in cages it actually grew faster than in similar cages at mid shore i.e. its potential niche included the low shore environment. When displaced to low shore in this experiment, however, the species showed directional movement away from low shore and back to mid shore. This movement is not directed by physiological, abiotic, tolerances at low water but must be caused by some limiting biotic factor which has selected for the evolution of homing behaviour in the species.

The results from Chapter 8 (Predation) suggested that predation pressure at low water could prove extremely detrimental to the maintenance of populations of L.obtusata at low shore. The prolonged, thin-shelled, juvenile stage of this species would be extremely vulnerable to crab predation. It was also noted, during the caging experiments, that L.obtusata being a macro-algal grazer reduced the fronds of F.serratus to tattered shreds at the end of the experimental period. This alga is temporally unreliable as it sheds its fronds during the autumn months and is subject to storm damage (Knight and Parke 1950, Smith 1973, pers obs). The natural loss of frond material when combined with extensive grazing would result in grave damage and loss of algal material from low shore. This evidence suggests that F.serratus would not provide an adequate food resource to maintain large populations of L.obtusata over an ecological time span.

The above explanation may account for reduced populations of L.obtusata at low shore, but it is probable

that predation pressure is the primary selective agent which has acted as an evolutionary force to drive homing movement of this species when displaced. The control by predation of habitat selection has been proposed for other species (Bovbjerg 1984; Levings and Garrity 1983; Underwood 1979). The potential niche of L.obtusata includes low shore and the environment there is not limiting in a physiological sense, but the biotic influences of predation (and possibly algal reliability) have acted as an evolutionary force to select for L.obtusata to be able to home from low shore to mid shore.

8.PREDATION

8.1 INTRODUCTION

Predation has long been accepted as a strong driving force in structuring ecological communities, and it has been shown to affect many aspects of the biology of individual species. It affects distribution both on a geographical and local scale (Behrens Yamada 1977; Chilton and Bull 1984; Heller 1976; Wilson,Crothers and Oldham 1983); morphology (Raffaelli 1978b; Crothers 1985(review); Kitching et al. 1966; Ebling et al. 1964; Heller 1976; Vermeij 1972) and community structure (Paine 1966, 1974, 1976; Menge 1976, 1978; Connell 1974; Fairweather and Underwood 1983; Petraitis 1987).

Littorinids are subject to such selection pressure from their numerous predators (see Pettit 1975 for detailed review). L.obtusata and L.mariae are preyed upon by four main predator groups: birds; fish; crustaceans; and dog whelks. Much of the literature on the subject describes flat winkles as L.littoralis or L.obtusata, and few authors have recognized L.mariae. It is reasonable to assume that, especially in the case of marine predators, L.mariae will be included in the diet of all those species that take L.obtusata.

Of the birds that prey on the flat winkles most are shorebirds. Purple sandpipers and Herring gulls have been seen to prey on L.littoralis (Pettit 1975, Sacchi 1961). Eiders and other sea ducks have been noted as taking L.obtusata and lacunids. Their diet would presumably include L.mariae if the species were present (Pettit 1975;

Goudle and Ankney 1986). Terrestrial predators of flat periwinkles include man (for decorative purposes) and possibly rats (Pettit 1975). The marine predators of these winkles are fish, crustaceans and dog whelks. Numerous fish species have been found to have littorinid shells in their gut contents. Of these the most important predators of flat winkles are Pollack (for L.littoralis), gobies and blennies (for L.obtusata and L.mariae - Pettit 1975; Reimchen 1974 and 1979). There are many records of the common shore crab, Carcinus maenas, preying on L.obtusata (Guiterman 1970; Reimchen 1974; Goodwin 1975; Crothers 1985; Pettit 1975). Many other species of crabs are known to prey on littorinids and it is assumed that species such as Cancer pagurus and Liocarcinus puber will take L.obtusata and L.mariae. Predation by Nucella lapillus will also affect both species (Crothers 1985 -where L.mariae is incorrectly called L.fabalis). Evidence for this predation can be found in the "drilled" shells of the two species left by the dog whelk. This list is by no means exhaustive as many earlier workers identified gastropods in gut contents as simply "littorinids" so it is probable that some other predators prey on L.obtusata and L.mariae. Of all the predators the two most important are thought to be the crab (Carcinus maenas) and the blenny (Blennius pholis).

Reimchen (1974,1979) has investigated the selective action of predation on colour polymorphism in L.obtusata and L.mariae. He claimed that visual selection by fish and birds accounted for the common colour morph of L.obtusata, green-olivacea, being predominant due to it being cryptic

on it s host weed Ascophyllum. The colour polymorphisms of L.mariae are also thought to be controlled via selective visual predation by the blenny. Reimchen showed that the yellow-citrina colour morph was cryptic to the blenny when viewed with light transmitted through the lamina of F.serratus. Blennies normally attack from the underside of the F.serratus fronds and so from this position citrina coloured shells are cryptic as compared to other colour morphs. The theory that visual selection affects colour polymorphism was further expounded to include the colour of recently hatched L.mariae, which Reimchen suggested cryptically resembled the tubes of Spirorbis. Reimchen's theory (1974) proposed that colour polymorphism would be maintained by density-dependent predation, blennies selecting conspicuous shells where snail density was high.

Both Guiterman (1970) and Reimchen (1974 and 1982) have examined the effect of crab predation on L.obtusata/mariae (Reimchen worked on both species but it is not clear from Guiterman's description whether he differentiated between the two). The selective action of crabs on littorinids does not affect the colour polymorphisms of the winkle species as crabs do not select their prey by visual stimuli but by tactile and chemical means (Crothers 1968). The effect of crab predation is thought to be seen in morphological selection on the littorinids. Guiterman and Reimchen suggested that there is a relationship between the exposure of the shore and the importance of crab predation. This is based on the fact that crabs are more prevalent on sheltered shores and has also been commented on by Raffaelli (1978) with respect to

L.rudis populations. Guiterman attributed the greater thickening of low-shore L.obtusata to selection by crab predation and suggested that the presence of larger shells at sheltered as opposed to exposed sites is a response that may lead to escape from predation.

Reimchen (1982) further developed this theory. He agreed that exposure is related to predation pressure from crabs and that this results in large-shelled L.obtusata. He improved this work by looking at the predation rate on different shell sizes of L.obtusata and L.mariae by crabs with different sized carapaces. He showed that the smaller, less thickened shells were taken by small crabs but that large shells could only be taken by very big crabs. From this he proposed that L.mariae's small size was a response that allowed escape from predation by shortening its time spent as a juvenile and rapidly growing to reach a thickened adult size, therefore decreasing the period in which it is vulnerable to crabs. This theory may be true in part but the full implication of Reimchen's work for the partitioning of the niches between L.obtusata and L.mariae was not developed.

Other work on the selective effects of crab predation on L.obtusata has been carried out by Seeley (1986). She showed by biometric surveys of museum specimens and by tethering experiments in the field that selection by crab predation had significantly changed the morphology of L.obtusata in New England. This piece of work is particularly elegant as it made use of the introduction of C.maenas into New England as a "natural" experimental manipulation of L.obtusata's morphological

response to predation affects.

The differing zonation patterns of L.obtusata and L.mariae will result in differing exposure to predation pressure by crabs and blennies. At low shore L.mariae will be exposed for longer periods of time to predation from the marine predators. L.obtusata at mid shore will spend less time exposed to marine predators, but more time exposed to terrestrial predators. It is possible that predation pressure from marine predators has in evolutionary terms, driven L.obtusata from the low shore zone, and that as Reimchen suggested (1982) L.mariae has been selected to be morphologically better able to withstand predation than L.obtusata. The enclosure of L.obtusata at low shore in cages from which predators were excluded has revealed that there are no physiological limitations preventing this species from living at this level. (See Chapter 6)

This chapter aims to investigate the effect of predation on L.obtusata and L.mariae at both mid and low shore. Using the tethering methods developed by Seeley (1986) the relative susceptibilities of the two species to crab attack were investigated. These experiments were aimed at elucidating the direction of selection pressure by the crab on different stages of the winkle species' development. The most susceptible stage of winkle life history is presumably that between the size that is too large to be preyed upon and the size that is too small to handle and therefore safe from predation. This section is aimed at elucidating the size ranges of the winkles that are most susceptible to crab predation and will determine whether there is an interspecific difference in predation

selection and how this might explain differences in the morphology and ecology of the two winkle species.

8.2 MATERIALS AND METHODS

8.2.1 CRAB ABUNDANCE

All field experiments were carried out at Sawdern in West Wales. To estimate the abundance and size range of crabs, collections were made on the shore. At both mid and low shore 30 minute searches were made for crabs by two people, and those found were scored and measured. The crabs were measured across the widest part of their carapace to the nearest 0.5mm using vernier calipers.

8.2.2 PREDATION SELECTION AT LOW SHORE

To investigate the selection pressure of C.maenas at low shore on the two winkle populations, tethering experiments were undertaken following the methods of Seeley (1986). To examine whether crabs foraged optimally (i.e. took the most profitable prey type) and to investigate the effects of this predation on the winkle species, different size ranges of both species were chosen using the data obtained from the biometric survey. For L.obtusata the sizes chosen were 7-10mm (juvenile unthickened individuals), and 14-17mm (adult thickened individuals). For L.mariae only one size was chosen, between 7-10mm (adult, thickened shells). These ranges allowed a comparison to be made between the susceptibility of the adult L.obtusata and L.mariae and juvenile L.obtusata to predation at low shore. The juvenile L.obtusata and the adult L.mariae were of a similar size and this tested whether crabs would have more of an effect on the thinner-shelled juvenile L.obtusata than the thickened adult L.mariae.

The experimental animals were divided into blocks of 6 (two individuals from each class as described above) and these were replicated 15 times (total=30 juvenile, 30 adult L.obusata and 30 adult L.mariae). Each winkle had a 1mm hole drilled into the shell lip using a hand-held drill with a dental burr. The winkles were then tied onto a 10cm piece of nylon monofilament fishing line and tethered to the base of a F.serratus plant as a group of 6. These were divided into blocks of five replicates and tethered to plants chosen at random at low shore. It was assumed that the location of crab predation would also be random.

8.2.3 PREDATION SELECTION AT MID SHORE

At mid shore the same experimental procedure was adopted except that only L.obtusata was used for the investigation. Two individuals (from each size range) were tethered either on the base of Ascophyllum plants or on the thallus. This experiment attempted to test the hypothesis that L.obtusata used floating fronds of Ascophyllum to escape predation. Each group consisted of 6 winkles (3 juvenile, 3 adult) and there were 2 replicates of each treatment (i.e a total of 24 experimental winkles). There was also a control similar to that described for the low shore experiment with a replicate series of winkles in a cage. These experiments were to be scored in the same way as the low shore experiment.

8.2.4 SCORING

These animals were examined after 2 days, 13 days, 29 days and then 74 days. To prevent shells being lost by the tethers becoming loose, or the shells breaking naturally, the winkles were tugged hard on their tethers

prior to starting the experiment to ensure shell and knot strength. Shells of juvenile L.obtusata (the thinnest of the classes) had a spot of Super-Glue applied to the knot to improve its integrity. To control further against inadvertent scoring of shells as taken by predation when they had been lost due to physical factors two extra replicates of the experimental blocks were placed in low shore cages (see Growth Rate Experiment, Chapter 6 for cage design). Cages effectively prevented predators reaching the winkles and therefore these shells were scored as controls for shells breaking or being lost from factors other than predation. When scored, the presence or absence of the shells was noted as well as any damage to the shells. The presence of a knot on any vacant tethers was also noted.

8.3 RESULTS

8.3.1 CRAB ABUNDANCE

Figure 8.1 illustrates the number and size ranges of the crab species found by two people in two 30 minute searches; one at mid shore and one at low shore. This shows that more crabs were found at low water than at mid shore. At low shore there were two species of crab found, Carcinus maenas (the common shore crab) and Cancer pagurus (the edible crab). Only C.maenas was found at mid shore. The numbers of C.maenas found at low and mid shore were very similar, the increase in numbers at low shore being due to the presence there of C.pagurus.

The sizes of the crabs found at the different shore levels also varied. At mid shore the maximum size found was 60mm, but very few crabs were larger than 35mm. The mean size found was 22.3mm (±9.6mm; n=70). In contrast, at low shore, the majority of C.maenas were above 30mm in size. The maximum size found was 75mm and the mean size was 43.6mm (±14.9mm ;n=75), almost double the mean value for mid shore. There were fewer C.pagurus found than C.maenas (n=33). The size-frequency pattern for C.pagurus was also less uniform than that for C.maenas. C.pagurus ranged in size from 15mm to 90mm. The sizes were divided into three distinct groups: between 15-35mm; between 40-65mm and finally between 75-90mm. The mean size for C.pagurus found was 49.9mm (±20.8), slightly larger than the mean value for C.maenas.

8.3.2 PREDATION PRESSURE AT LOW SHORE

The results from the tethering experiment are shown

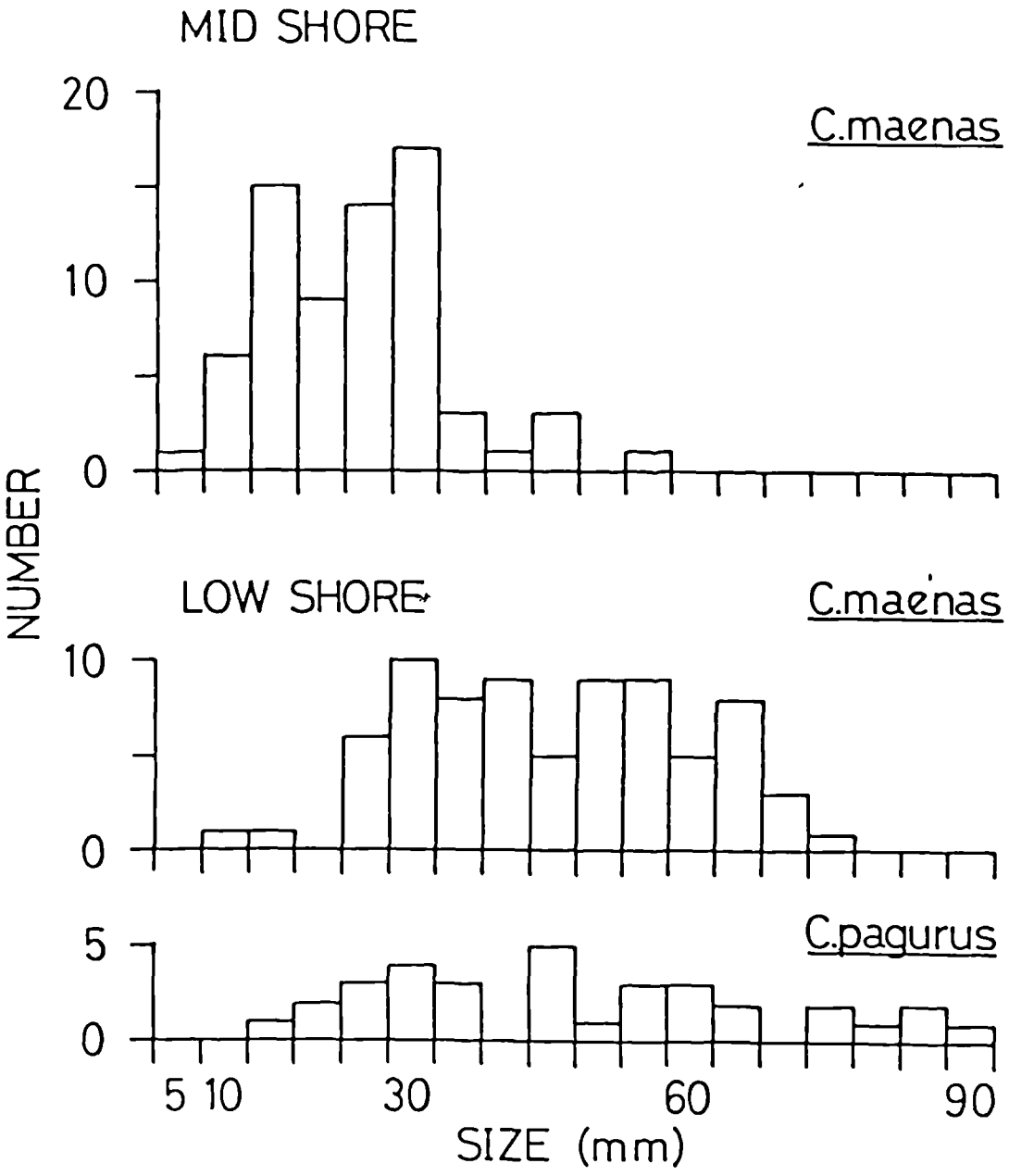


Figure 8.1
Size frequency histograms for crabs found in 30 minute searches at mid and low shore at Sawdern, 15 June 1987.

in Figure 8.2 and Table 8.1. It can be seen that initially, after 2 days, more L.obtusata juveniles were eaten than either adult L.obtusata or L.mariae. This situation altered after 15 days when more L.mariae were taken than L.obtusata juveniles, but again less adult L.obtusata were lost than either of the other two classes. The differences between the numbers of the three classes actually taken were slight. After 29 days the order of preference was identical and the differences between the treatments remained constant. After 74 days one set of tethers was lost; of those remaining none had any juvenile L.obtusata left on them. There were a few L.mariae and adult L.obtusata left, slightly more L.obtusata than L.mariae. A Chi-square test to investigate the hypothesis that the different classes were taken randomly was not disproved. This does not therefore provide evidence that predation on the different winkle classes was other than random.

8.3.3 PREDATION PRESSURE AT MID SHORE

At mid shore one of the replicate treatments was lost after 13 days. This negated the statistical validity of the experiment so only inferences can be made from this experiment. After 29 days all the juveniles had been taken, and all the adults were still intact.

8.3.4 SCORING

Winkles in all the control cages stayed on their respective tethers (a total of 10 adult and 10 juvenile L.obtusata, and 4 adult L.mariae) until 74 days when one juvenile L.obtusata was lost. As the winkles shells had grown over the tethers they were more secure so it was

Table 8.1
Cumulative numbers of winkles lost, and results of Chi-square Test to investigate if there was any difference in the loss rate between the treatments.

TREATMENT	DAY 2	DAY 17	DAY 30	DAY 74
L.mariae	2	16	19	23
juvenile L.obtusata	8	18	21	28
adult L.obtusata	5	19	22	24
TOTAL LOST	15	53	62	75
Chi-Square value	3.8 N.S.	0.17 N.S.	0.12 N.S.	3.7 N.S.

KEY
N.S. = No significant difference in the loss rate between the treatments

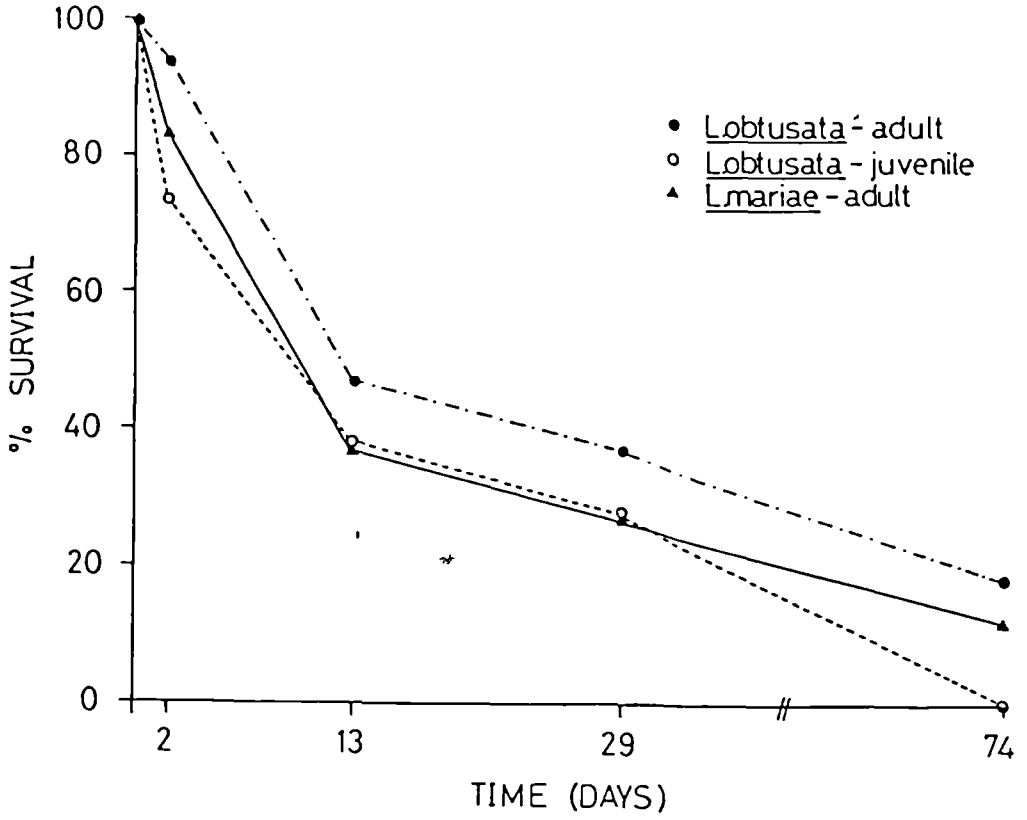


Figure 8.2
Percentage survival of littorinids tethered at low shore, Sawdern. Starting date was 14, June 1987.

concluded that this loss was due to handling damage associated with pulling the sample out of the cage to score. In general the tethers on all the winkles became more reliable as the experiment continued. In all the experimental checks only once was evidence for loss due to non-predator action noted (a single juvenile L.obtusata at low shore- this was subsequently taken into account in the analysis of the data). Towards the end of the experiment (after 30 days) some tethers had lost their knots, and the wire seemed to be severed. This did not affect the results as in most cases the experimental animals had previously been lost from these tethers. After 74 days one set of tethers was completely lost and these were therefore not included in the subsequent analysis.

8.4 DISCUSSION

8.4.1 CRAB ABUNDANCE

The sampling of crab size and distribution at mid and low shore showed a large difference between the tidal heights. Not only did the low shore area have two species of crabs, C.maenas and C.pagurus, but these were larger and more numerous than the C.maenas found at mid shore. This difference means that winkles at low shore will be subject to more intense predation pressure than those at mid shore. The principal crab predator at these levels was C.maenas.

The autecology of C.maenas is well understood through the work and review of Crothers (1967,1968 and 1970). The active population is made up of three components (called A,B and C by Crothers). A and B are the only components of interest in this study as crabs in component C remain principally offshore and therefore will not affect winkle populations. Component A crabs remain on the shore for the entire tidal cycle during the summer, where they hide beneath rocks and algae, foraging at high tide. These crabs have a carapace size of below 35mm. The crabs found at mid shore in this study were from this component. Component B crabs migrate with the tide from low water onto the shore to forage and then retreat with the tide. Some crabs from this component will also affect winkles at mid shore. The crabs in component B are larger than those in A. The crabs found in this study at low shore were made up of individuals from this component and that of A. The sample at low shore will have slightly underestimated the size and frequency of crabs at this

level as more would migrate on shore when the tide rises. This suggests that there is increased predation pressure at low shore as compared to mid shore. The nature of this pressure will also be different as there will be more crabs, of two different species, and of varying sizes.

Many workers have discussed the increase in predation pressure low on the shore as compared to mid/high shore areas (Chilton and Bull 1982; Guiterman 1970; Reimchen 1974; Paine 1966,1974; Connell 1972,1974; Menge 1978, 1983; Fairweather 1985). This increase is due to a general increase in the numbers of predators (more crab and fish species in this case) and also an increase in the effectiveness of the predator, either due to increased foraging times or because of *increased efficiency resulting* from an increase in body size of the predator. Numerous authors have shown that the ability of crabs to handle prey items is a function of their body size (Reimchen 1982; Crothers 1986; Elner and Hughes 1974; Zipser and Vermeij 1978). At mid shore there are, potentially, the same number of predator species present. Predation pressure is reduced, however, because the predators are usually smaller and have short foraging periods available (as a result of mid shore having relatively long emersion times). Predation pressure at low shore is therefore a much more important factor in community structure and species ecology than it is at mid shore.

8.4.2 PREDATION SELECTION AT LOW SHORE

The evolutionary ecology of predation can be studied from the strategies of the predator and those of the prey. The predator should aim to maximise the rate of energy

uptake that it can achieve during its foraging time. As with all such interactions the predator has to locate its prey item, ready it for consumption and then eat it. The net amount of energy gained from this operation is the measure of the predator's success (Krebs and Davies 1986; Elner and Hughes 1974). In this experiment it was proposed that if crabs foraged optimally, then they would prey on the winkle classes in the following order: juvenile L.obtusata first (thin shelled, medium meat yield); then L.mariae (thicker shelled, less meat yield);and finally adult L.obtusata (very thick but high meat yield). These predictions assume that the predators have to expend energy/time on handling the winkles (i.e. cracking the shells) to obtain the meat and that they are able to predict the value of the prey item.

The tethering experiments showed, however, that at low shore there was no preference by predators for any of the winkle classes,i.e adult or juvenile L.obtusata or L.mariae. It appears that all the winkle classes were taken to the same extent, although there was a slight fluctuation in the degree over the time period concerned. In the case of the first sample, after 2 days, adult L.obtusata were preyed upon slightly less than the other classes. This could be related to the increased size and thickness of these adults, which only large crabs can overcome. As the experiment continued to run, larger crabs presumably encountered the adult L.obtusata and were able to crack the shells and eat the winkles. The trend for adult L.obtusata to be preyed on less than the other two classes continued throughout the experiment. This suggests that

adult L.obtusata are better able to survive at this level than the more vulnerable juveniles and L.mariae. The lower incidence of deaths of adult L.obtusata was probably a function of the number of large crabs (i.e. those capable of crushing the shells) that encountered the individuals. Even at the end of the experiment adult L.obtusata were preyed on less than any of the other classes. As predicted juvenile L.obtusata were preyed on the most, with none being present at the end of the experiment. L.mariae was also more heavily predated than adult L.obtusata. Despite these trends there was no statistical difference between the varying winkle treatments.

The lack of difference between predation on L.mariae and juvenile L.obtusata may be explained by the fact that crabs were not foraging optimally in this experiment. The experiment was largely artificial in that juvenile L.obtusata would have been a novel prey to the crabs, since adult L.obtusata are rarely found in dense numbers at low shore, except after a storm, and juveniles are even less frequent (pers.obs). The crabs would therefore have undergone no period of learning or decision-making, and the winkles would have had an unpredictable value as prey items. It can be assumed that the crabs will be generalists and attempt to eat any winkle that they encounter (see Elner and Hughes 1974). This agrees with the reports of Hughes and Elner (1979) for C.maenas foraging on dogwhelks and Rangeley and Thomas (1987) for C.maenas taking L.littorea and L.obtusata. The success of the crab in handling any winkle will depend on its size (and therefore crushing ability) relative to the winkle's

physical defence. The data suggest that the largest crab sizes seen in the field would have had no trouble in crushing any of the winkle classes and were probably only limited by their encounter rate with the prey item. The experiments were therefore testing the relative merits of the winkle's adaptations against predators.

The predator's mode of action can be summarised below.

(1) SEARCH

(2) ENCOUNTER PREY ? YES (GO TO 3) / NO (GO TO 1)

(3) HANDLE PREY (i.e CRACK) ? YES (GO TO 4) / NO (GO TO 1)

(4) EAT BACK TO (1)

This scheme allows the prey item two main escape routes; either to avoid being encountered by the predator, or to be protected physically so that the predator is unable to handle it sucessfully. An increase in the density of large crabs might then lead either to increased selection for shell defence (to reduce the ability of the crabs to handle the prey sucessful), or to avoidance of the predator.

There are many cases in which prey defence against predator handling has been demonstrated. Chilton and Bull (1982) recorded an increase in shell size of Nerita, Bembicium and Austrocochlea species along the vertical gradient of the shore in response to predator selection by crabs. Selection for physical adaptations to predation pressure is strong and have been recorded in many species: limpets (Lowell 1986), Nucella species (Ebling et al. 1964, Kitching et al. 1966); Tegula species (Watanabe 1986, Schmitt 1981) and gastropods in general (Underwood 1979, Zipser and Vermeij 1978). Guiterman (1970) suggested

that the increased thickening of the shell of L.obtusata lower on the shore was a response to predation pressure. Reimchen (1974) has suggested the high degree of thickening and small aperture of L.mariae to be similar responses to low-shore predation pressure. The force of this selection pressure has been eloquently demonstrated by Seeley (1986) who showed that selection pressure by C.maenas has affected shell form of L.obtusata in North America. The adaptive thickening by both species will remove some individuals from the diet of small crabs which might otherwise be able to crush a similarly sized but less thickened shell. This was demonstrated by Reimchen (1982) in the laboratory when small (15-30mm carapace) C.maenas preferentially cracked L.obtusata juveniles as opposed to L.mariae of a similar size. In the summer, at low shore, this adaptation would be of limited use due to the high frequency of large crabs. The tethering experiments demonstrated this; indeed, predation on the scale seen in this experiment would prove extremely detrimental to populations of both species. Populations of L.obtusata at low water would probably not exist for any period of time. Selection pressure from predation may maintain the lower limit of L.obtusata at mid shore. As the physical adaptations of L.mariae were inadequate to prevent predation by large crabs during the summer, to maintain a population at low shore L.mariae must overcome this problem in some other way.

The alternative to adapting a defence against predator handling is to avoid being encountered. This can be achieved both spatially and temporally. There are many examples in the literature of prey species escaping from

predators by movement. Many species of Tegula escape predation from starfish by fleeing (Schmitt 1981,1982; Watanabe 1983). These species have been shown to have very specific responses to different species of predator. For example, one species will flee from one starfish but will remain active in the presence of another, having developed a chemical distasteful to that species (Watanabe 1983). Such specific recognition of predators has also been demonstrated for Littorina unifasciata which reacts to whelk species (McKillup 1982). Often a species is forced to find a behavioural refuge from predation when it is unable to reach an escape based on size or morphological adaptation. Such a situation has been seen in Nerita species which have a complex relationship with two predators, fish species and Purpura, both of which they attempt to avoid in time and space by varying activity patterns (Garrity and Levings 1981). Littorina irrorata escapes predation from crabs and conchs by climbing the stalks of tall grasses at low water to gain a refuge from foraging predators. This was demonstrated using tethered and caged snails at different heights on the grasses (Warren 1985). Climbing allowed the winkle a circatidal escape from predation. The predators in this example showed a seasonal fluctuation in their activity, both the crabs and conchs migrating offshore in the winter months. L.irrorata therefore escaped predation both in time and space. Variation in predation intensity due to seasonal variation in predator activity is an effective escape for some prey species.

C.maenas shows a seasonal variation in its onshore

activity (Crothers 1968, Atkinson and Parsons 1973). In the summer months (April-October) the majority of the crabs were in section A and B of the population as shown in this investigation. During the autumn there is a mass movement offshore from these components of the crab population to join section C. The crabs overwintered in this component, showing reduced foraging activity (Atkinson and Parsons 1973). Activity increases towards the end of winter and the crabs begin foraging and return to the shore in March of the next year. If the pattern observed for the population dynamics of L.mariae is generally true for sheltered shores then the species "escapes" from intense predation pressure during the winter as winkles begin to reach sexual maturity. The months when copulation and egg laying reach a peak coincide with reduced crab predation pressure. It is possible that the very small juvenile L.mariae also escape predation because they are too small to be found or handled. This has been suggested for small gastropods (Zipser and Vermeij 1978) although there is no evidence in the present study to support this. Rangeley and Thomas (1987) noted that large adult crabs had difficulty handling the smaller sized L.obtusata. In the small size range, thickening of the shell by L.mariae might prove effective in making the species unable to be handled by the smaller crabs. On very sheltered shores there is a tendency for L.mariae to decrease in mean size, possibly due to a selected adaptation to prevent effective crab handling.

The annual life cycle shown by L.mariae on sheltered shores such as Sawdern provides a temporal escape from the

effects of predation. In the spring and summer months, when L.mariae's egg masses hatched, the C.maenas populations returned to the shore to forage. Predation from this crab and other predators may account for the high juvenile mortality, and death of the remaining adults seen. The high numbers of juveniles were lowered as a result of mortality factors, and few L.mariae survived into the autumn months. Those that did were approaching maturity and were between 7-11mm. Winkles of this size would be extremely vulnerable to predation by crabs, but predation was avoided because at this time of the year the majority of large crabs migrate offshore. Any crabs left on shore would be in component A of the population, and these animals would be too small to overcome the thickened shells of the adult L.mariae. The remaining L.mariae were therefore able to breed and produce egg masses in the winter months, suffering only minor predation before the majority of crabs returned to the shore in the spring. These months represent extremes in the physical environment with winter storms and low temperatures. Despite this, sufficient adults survived to produce a large number of egg masses. In the spring the egg masses hatched out and the juveniles began to grow. The seasonal migration of C.maenas back onto shore took place and both the remaining adults and juveniles of L.mariae suffered heavy mortality. The previous years adult L.mariae did not survive past August.

As previously mentioned, if L.obtusata were to live at low shore, the intensity of predation would have a profound effect on its population dynamics. As L.obtusata

does not reach sexual maturity until approximately 18 months after hatching there would be no temporal escape from predation to allow breeding in the first year of life. The previous year's recruits would be reaching 10mm in size in late February, and they would suffer intense mortality from the returning C.maenas. This would effectively prevent the majority of the juvenile L.obtusata from being recruited into the sexually mature component of the population and within a few years the population would become non-viable at this shore level. It should be considered that on sheltered shores such driving selective pressure may *account for the niche partitioning of* L.obtusata and L.mariae.

Predation pressure has been suggested to be an important selective force on the evolution of life strategies (Miller 1979). It has been suggested that unpredictable predation pressure selects for early maturation and increased reproductive efficiency, in an attempt by the prey to reproduce before predation is effective (Vermeij 1972). This results in the life history of the species following that of a conventional "r" strategist. This is the case as seen for L.mariae (see previous chapter), which being subject to intense predation pressure has evolved small body size and a life strategy which allows the species to breed and reproduce before predation can seriously affect the species. The converse is true for L.obtusata, which does not suffer from such intense selection and therefore its life cycle follows a more "K" type strategy. This species is restricted from widening its zone by the pressure of predation lower on the shore.

9. GENERAL DISCUSSION

The debate concerning the specific status of the flat periwinkle group is still continuing. The inclusion, or exclusion, of further species in the complex has been suggested: for example the inclusion of a species of dwarf L.mariae (Reimchen 1981; Nielsen 1980); and the exclusion of L.palliata (Warmoes 1986) and L.aestuarii (Moyse et al. 1982). In this study only two species were considered, L.obtusata and L.mariae. That these are two species, sensu stricto, is beyond doubt as has been shown by morphometric, ecological and genetic investigation (Sacchi and Rastelli 1966; Reimchen 1974; Goodwin 1975; Wilkins and O'Regan 1980; Morris 1979).

L.obtusata and L.mariae have both been shown to exhibit environmentally induced morphological variation (Sacchi 1967; Reimchen 1974; Goodwin 1975). However, the two species show different trends in size at sheltered and exposed sites. The adult size of L.obtusata increases as shores become more sheltered, but decreases when shores are more exposed. The opposite is seen for L.mariae; this species is smaller at sheltered sites as compared to more exposed sites. The results of multivariate analysis in this study further illustrated these clines of variation between populations at different sites. This is to be expected as species which have a very limited dispersal potential (laying benthic egg masses) will exhibit selective variation under different environmental regimes. This was not investigated further as the introduction of a further complicating factor would make the project too

ambitious. It was decided to concentrate on the ecology of the two species on sheltered shores. The morphological variation of these species along the exposure gradient is a subject worthy of further work. As has been shown with L.saxatilis (Janson 1982, 1983, Janson and Sundberg 1983, Janson 1985, Ward and Janson 1985), differing morphologies, which are genetically controlled, can represent clines of variation associated with differential selection pressure induced by the environment.

In this study, therefore, only two species were present, L.obtusata and L.mariae. The two species were shown to exhibit the morphometric differences described by previous workers (Sacchi and Rastelli 1966; Reimchen 1974; Goodwin 1975; Goodwin and Fish 1977) having different sized shells, differences in penial morphology, colour morphs, and sex ratios (Chapter 3). Once this had been ascertained ecological work on the two species could be undertaken with confidence. The biometric work also allowed the perfection of field identification of the two species. As a consequence of experience gained by dissection in the laboratory, the winkles could at many sites be assigned to species in the field by colour morph and shore level (L.obtusata being olivacea and L.mariae citrina/reticulata). At other sites (Porlock), and in the case of juveniles, identification was more difficult. In these cases winkles were identified using the sculpturing on the periostracum (Reimchen 1974). At Sawdern, the site used for most of the ecological work, identification was relatively simple as L.obtusata were olivacea and L.mariae were citrina; juveniles could be assigned to either species

by a slight variation in colour and the sculpturing of the periostracum.

The first aim was to establish the realized niches occupied by the two species on a number of shores. By investigating the vertical partitioning of the shore the spatial separation of the niches of the two species could be examined. The results of these vertical transects (Chapter 4) showed that there was a distinct vertical partitioning of the shore: L.obtusata was found at all the shore levels whilst L.mariae was limited to the low shore area. Detailed investigation of the distribution patterns of the two species revealed a number of niche dimensions. L.obtusata was found at its most dense at mid shore on Ascophyllum nodosum. Extension either upshore or downshore resulted in a decrease in the numbers found as the species extended outside its optimum niche. L.mariae was limited to living exclusively on F.serratus.

Ascophyllum is a perennial alga living for perhaps 100's of years (Cousens 1981, Baardseth 1970). Shores colonized by this species tend to develop dense stands of the alga which provide a temporally stable resource for L.obtusata. The relationship between L.obtusata and Ascophyllum is very complex; L.obtusata is actively attracted to the algae despite the production by Ascophyllum of secondary plant compounds which other grazers find repulsive (Watson 1983; Gieselman and McConnell 1981). L.obtusata is not, however, limited to this alga as a substrate on which to live; but in the present study its peak of distribution was always correlated with the presence of Ascophyllum. L.obtusata

uses the alga as a substrate on which to live and reproduce; most of its egg masses are laid on this alga (Goodwin 1975). Previous workers have disagreed as to whether L.obtusata actually grazed on the algal tissue (Watson 1983; Petraitis pers. comm.) or whether it grazed micro-epiphytes off the frond surface (Menge 1975). Evidence from this study showed that L.obtusata does actually eat Ascophyllum, confirming the findings of Watson and Norton (1987). The results of adult grazing can been seen as gouged areas on the surface of the algal fronds. The exact diet of both species of flat periwinkle is worthy of further investigation and it is quite possible that juveniles of L.obtusata eat micro-epiphytes or algal reproductive tissue which is more readily edible than the frond tissue of Ascophyllum (Watson 1983 ; Watson and Norton 1987). Relying on a diet composed, primarily, of micro-epiphytes living on Ascophyllum would be an unstable strategy on British Coasts. Ascophyllum is known to support few epiphytes apart from Polysiphonia (Round 1984); and also prevents epiphyte colonization by frequently shedding its epidermis (Filion-Myklebust and Norton 1981). Heavy epiphyte loading has, however, been recorded in America during the fall and this may provide an important food resource, especially for L.obtusata juveniles (Menge 1975).

The realized niche of L.mariae is very different from that of L.obtusata. Inhabiting the low shore area, L.mariae is exclusively confined to F.serratus as its host alga. This alga forms patches and clumps of plants on the low shore area. F.serratus is a far less reliable resource

than Ascophyllum as it is subject to frequent storm damage and seasonal defoliation (Knight and Parke 1950, Smith 1973). This results in the loss of frond surface area for the winkle to utilise. Like L.obtusata, L.mariae lays its egg masses primarily on its host alga, in this case F.serratus (Goodwin 1975); it does not graze the alga itself but browses micro-epiphytes off the frond surface. As F.serratus supports far more epiphytes than Ascophyllum (Round 1984) this provides a satisfactory although seasonally variable resource for L.mariae to exploit. The frond surface of F.serratus, as an area for epiphytic growth and settlement, is therefore a more important resource for L.mariae than the algal tissue itself.

Chapter 4 showed that the two species have very different realized niches. L.obtusata is primarily a macro-algal grazer and inhabits a wide realized niche along the vertical gradient of the beach. Its optimum niche is at mid shore on Ascophyllum as a host alga. L.mariae, on the other hand, inhabits a far narrower niche; being restricted to F.serratus off which it browses micro-epiphytes. Therefore, not only do the species exhibit spatial partitioning, but also trophic partitioning of the intertidal environment.

The investigation of the population dynamics (Chapter 5) of the two species also revealed significant differences in their ecologies. L.obtusata, as shown by previous workers, has a perennial life cycle (Goodwin 1978; Guiterman 1970; Hollingworth 1981; Daguzan 1976). Individuals live for 3-4 years; egg masses hatching in the spring and juveniles growing to reach 10-12mm by their

first winter, during which they show a growth quiescence. After this period the juveniles continue to grow and reach adult size by autumn of the next year. The juvenile stages are characterized by thin lipped shells and many juveniles seek refuge in damaged air bladders (Reimchen 1974). The sexually mature adults have fully thickened shells and live for 1-2 years. Such a long period of development before reproduction requires constant and reliable resources. This is provided by fucoid algae, especially Ascophyllum.

L.mariae, in contrast, exhibits on the sheltered shores examined an annual life cycle. There is a large input of juveniles in the spring which rapidly grow to reach maturity in autumn. Mortality during this period is extremely high, showing an exponential decrease in numbers typical of a survivorship Type III curve. Few individuals, mostly adults, overwinter and reproduce to allow a large influx of juveniles next spring when the remaining adults die off. This life cycle is typical of a traditional "r" selected species and may account for the small body size of L.mariae, as has been demonstrated in other species which have short development times (Spight and Emlen 1976; Calder 1984; Miller 1976,1984) and high reproductive outputs. The differences between the life cycles of the two species are related to their differing body sizes. A long life span allows L.obtusata to achieve a larger size than L.mariae, and to have a more complex life history involving a prolonged juvenile stage. L.mariae, living for only one year, grows at its maximum rate to reach full body size and sexual maturity by the end of its first year.

The life cycles of the two species are closely

linked to their host algae. L.obtusata, becauses it lives on Ascophyllum, has a reliable food source which will support a complex life history; whereas L.mariae has to rely on the fluctuating resource of micro-epiphytes on F.serratus fronds which themselves are subject to seasonal loss. The variation in F.serratus populations has been noted by many other authors (Knight and Parke 1950, Smith 1973), and has been linked to the annual life cycle of Lacuna pallidula (Smith 1973). This species is more strictly annual than L.mariae and has been investigated at many sites (Smith 1973, Grahame 1977,1985;). The life history of L.mariae has only been investigated at one site and needs to be verified at others. It is possible that this phenomenon is only seen on very sheltered shores where it has been noted as regularly occurring (R.G.Crump pers. comm).

The exploitation of the realized niches of these two species is therefore very different and it is possible that the limitations imposed by their differing habitats account for the morphological differences between the species. To investigate this in more detail and to elucidate factors controlling the niche partitioning of the two species the transplant experiments discussed in Chapter 6 were undertaken. These were aimed at examining what the effect of extending the realized niches of the species would have on their success.

Transplanting L.obtusata, in cages (and therefore removing the effects of predation), outside its realized niche to L.mariae's shore level actually improved the growth of the species. At this level L.obtusata was able

to feed for longer on an alga which is more easy to exploit than Ascophyllum (Watson 1983). This experiment showed that the low shore environment is within L.obtusata's abiotically controlled potential niche. The mid shore area, however, was outside the potential niche of L.mariae. When transplanted to this level a large number of L.mariae died; and the growth rates of the survivors was depressed. This may be due to limiting food availability, the lack of epiphytes and the structure of the Ascophyllum fronds which are extremely tough to excavate (Watson 1983). Other factors such as the more extreme physical conditions at mid shore may inhibit L.mariae. Laboratory work by Sacchi (1972a and b) has shown L.mariae to be more susceptible to extremes of physical conditions than L.obtusata. Mid shore is therefore outside the potential niche, as dictated by physical, abiotic factors of L.mariae. Such limitations to the zonation patterns of marine species have previously been noted. The upper limits of marine species are most often controlled by physical factors (Wolcott 1973; Hawkins and Hartnoll 1985); as is the case for L.mariae. The lower limits are more often controlled by biological factors (Paine 1966; Schonbeck and Norton 1979) and it was assumed that the limits of the realized niche of L.obtusata must be set by some biotic factor that was absent from the cage experiments. To investigate whether there was a behaviourally mediated selection for the shore level inhabited by the two species the movement experiment described in Chapter 7 was carried out.

The results from this showed that both L.mariae and L.obtusata orientated and moved towards their home zones

when transplanted; movement being greater at mid shore, especially for L.mariae. This confirms that there is a selective advantage for the species to inhabit their respective tidal zones which has resulted in the evolution of behavioural responses to maintain that level. Evidence from previous work points towards the host alga as being the limiting factor which would select for the homing behaviour (Ebbinge Wubben quoted by Barkman 1955; Underwood 1972a; 1979). Both L.obtusata and L.mariae are attracted to their host algae and it is possible that the algae represent a limiting resource for both species. This is, however, unlikely to be the overriding evolutionary reason, especially in the case of L.obtusata.

The notable biotic factor removed from the caging experiment was predation. The role of blennies and crabs in the life histories of L.obtusata and L.mariae have been examined in some detail (Reimchen 1974; 1979; 1982). To investigate the effects of crab predation by C.maenas in the field the experiments described in Chapter 8 were set up where tethered individuals of L.obtusata and L.mariae were kept at low shore.

The results suggest that predation by crabs is an important factor in the niche partitioning of L.obtusata and L.mariae. Predation pressure from crabs is greater at low shore than mid shore and will be most effective on thin shelled individuals. L.obtusata avoids this selective pressure by living at mid shore where smaller crabs are active and account for some juvenile mortality; but not enough to represent a danger to recruitment to sexual maturity. Adult L.obtusata are generally too large to be

preyed upon by the relatively small crabs found at this level. L.mariae is subject to the maximum predation pressure at low shore and its life style minimises the vulnerable thin shelled stage of its development, growing quickly and therefore remaining small in size but greatly thickened. Small individuals are more difficult for large crabs to handle (Zipser and Vermeij 1978; Rangeley and Thomas 1987) and small crabs find the shell too thick to crack (Reimchen 1982). As L.mariae approaches adult size and starts to breed, there is a temporal relaxation of predation pressure while the crabs migrate offshore and foraging activity onshore is reduced. If L.obtusata were to be exposed to this pressure at low shore then it is possible that the species would become locally extinct. The long time spent as a thin shelled juvenile would be extremely vulnerable to crab predation. Predation therefore could account for the lower limits of L.obtusata's extension downshore.

GENERAL CONCLUSIONS

Traditional ecological theories that niche displacement between two similar species is the result of competitive exclusion are now under review (Den Boer 1986). Previously it has been assumed that competitive displacement between similar species would drive the competing species to niche partitioning, or indeed subsequent speciation. Such theorising has often been called upon to explain the close similarity between the niches of congeneric species; but as Connell argues (1980) the "ghost of competition past" is all too often invoked with little or no evidence for its involvement.

This study has shown little evidence for competition between L.obtusata and L.mariae in situ. When forcibly maintained in mixed stands there is evidence to suggest that the macro-algal feeding of L.obtusata will graze away most of the F.serratus fronds to limit L.mariae's browsing surface; the two species would be competing for the algal frond surface. This never occurs naturally, however, because L.obtusata shows a behavioural adaptation to "home" to mid shore when displaced to low shore. This response is thought to be mediated through the attraction of the species for its host algal species; exudates from Ascophyllum providing the stimulus by which the species orientates. But is this the selective force which has driven this niche selection ? It is possible that food availability is important in this selection and that this has driven L.obtusata upshore onto Ascophyllum and has kept L.mariae at low shore on F.serratus. This is doubtful as the overriding factor, however, as L.obtusata is capable of living on a number of fucoids, and its zonation pattern, especially on semi-exposed shores, encompasses low shore algae.

There is evidence to suggest that the major selective force which accounts for the niche partitioning of L.obtusata and L.mariae is predation. Anti-predator needs have recently been recognized as major factors in determining the niches of species (Sih et al. 1985). Escapes from, or avoidance of, predation are seen as important factors in niche partioning and displacement between species (Sih 1987; Hairston 1987; Den Boer 1986). In the case of L.obtusata and L.mariae the "ghost of

predation past" may account for not only the differences in shore level inhabited but also differences in their life histories and morphologies.

Visual predation by blennies has been proposed as an important selective force acting on the colour morphs of L.obtusata and L.mariae (Reimchen 1979). Evidence to illustrate the effect of predation on the shell morphology of these species has been proposed by Seeley (1986). Working in North America Seeley has shown a change in the shell morphology of L.obtusata as a response to the predation effects of C.maenas. Since the introduction of C.maenas to New England in the late 1900's the shell of L.obtusata has become thicker and also lower spired; indeed the shell now closely resembles that of L.mariae in Britain. The absence of L.mariae (Seeley pers.comm) on the East Coast of the U.S.A means that there is an empty niche available for an anti-predator escape of the type shown by L.mariae on British Coasts. Seeley did not investigate the ecologies of the L.obtusata populations under differing predation pressure and it is possible that this is an area worthy of further work.

Seeley's work has illustrated a change in morphology due to selection pressure from predation. It follows that such pressure may have driven L.obtusata to adopt the complex life history recorded at mid shore where its juvenile stages would be relatively safe from predation; and where its adult stages would be immune to predation from the small crabs found at that level. L.mariae has been selected to adopt a different strategy, remaining small but thickened and therefore being protected from

small crabs. L.mariae also achieves a temporal escape from predation pressure whilst reproducing (see Sih 1987 for details of escape responses in time and space). It is probable that predation also accounts for the lack of overlap between the vertical zones of the two species: the degree of overlap is greater on exposed shores where predation is reduced. Predation is presumably the selective force driving the movement patterns shown by the two species when displaced from their home zones. This homing movement removes L.obtusata from low shore when displaced there and will accordingly result in avoidance of competition between the two species for F.serratus fronds.

The differences in the ecologies of the two species can probably be accounted for by the effects of anti-predator needs as opposed to competitive displacement. The selection for different anti-predator responses has resulted in niche displacement and subsequent specialization of L.obtusata and L.mariae.

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